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SOIL PHOSPHATE AND VEGETAL PATTERN IN SOME NATURAL COMMUNITIES OF SOUTH-EASTERN QUEENSLAND, AUSTRALIA[1]

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INTRODUCTION

Beadle (1953) refers to the restricted interest in the effects of individual properties of the soil on communities of native vegetation. The literature on soil phosphate includes few attempts to study it in this connection, the only recent work seen by us being that of Allard (1942), Billings (1950), Beadle (1954), and Salisbury (1954).

When selecting and developing areas for planting to exotic species of *Pinus*, the Queensland Forest Service uses a set of criteria which includes the total phosphate content of the upper 4 inches of soil and the frequency and vigour of the native trees, chiefly species of *Eucalyptus* L'Hérit. The second criterion is not recorded by any system of formal ecological classification, but from experience gained by one of the authors (Coaldrake) during an ecological study of the region, the original survey data may be transformed into floristic groups which are distinct units in the field. When these are coupled with the large number of phosphate records the hypothesis that soil phosphate governs vegetal pattern can be examined statistically for the areas sampled.

The phosphate/vegetation records used in this study come from two areas twenty miles apart. The more southerly of these is at the Toolara Forest Station, approximately 20 miles east of Gympie, while the other is at the Tuan Creek Forest Station, 10 miles south-east of Maryborough (Fig. 1). Through the courtesy of the Director of the Queensland Forest Service, the authors have been able to study the results of 940 phosphate analyses.

[1] The authors acknowledge the generosity of the Director of the Queensland Forest Service in making available the phosphate data and survey records used in this study. They are also grateful to Mr. G. W. McHarg for considerable assistance in regrouping the data and preparing the maps.

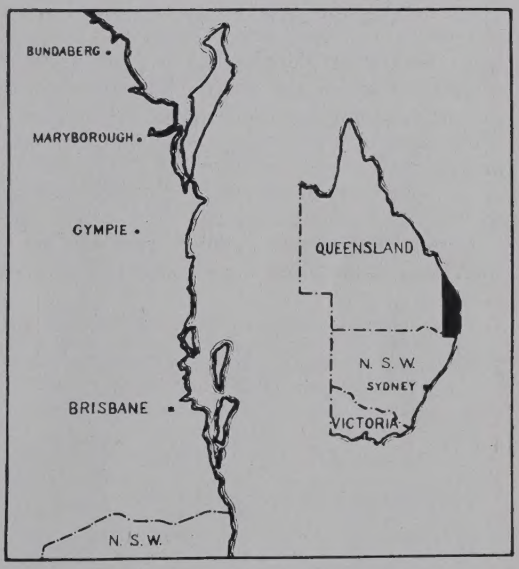

FIG. 1. Map of the general region.

SAMPLING AND CHEMICAL ANALYSIS

The samples from Toolara were collected in two batches. In the first area (Toolara A) the soil was sampled at every intersection of a 10 chain grid. In Toolara B and at Tuan Creek sites considered as unsuitable for planting to *Pinus* were not sampled. At each site sampled 4 cores 1 inch in diameter, 4 inches deep, and free of litter were collected. These were bulked and analysed for total phosphate by the Lorenz gravimetric method (Tuan Creek) and by a colorimetric method[2] (Toolara). The two methods give comparable results.

[2] Developed by J. T. Hutton, Division of Soils, C.S.I.R. O., Adelaide, Australia.

While the system of recording vegetation and the varying density of sampling were not ideal for this study the location of the sampling sites used was unbiased by any precognition of this study. The varying density of sampling is overcome by the statistical treatment chosen.

Soils and Vegetation

The soils and vegetation of this region will be described in some detail by Coaldrake (papers in preparation). Similar soils in the southern part of the same region have been described by Hubble (1954). The soils chiefly concerned here may be described as deep lateritic podzolics formed under climatic conditions in which summer rainfall is dominant and coupled with high humidities. They are derived from upper Triassic quartzose sandstones of the Landsborough Series (Bryan and Jones, 1945) whose origin is still conjectural. One community (*Eucalyptus seeana* type) occurs on gleyed soils in drainage lines, while the treeless type occurs either on a gleyed soil or, in a few cases, on a groundwater podzol. While there is chemical variation in these soils the type and range of variation tends to uniformity in the upper part of the solum; physical variation seems to be more pronounced. The surface horizon from which these samples are taken varies from loamy sand through sandy loam to fine sandy loam. The majority have a sandy loam texture.

Table I. Vegetal categories used in the statistical analysis together with their classification at the level of the formation and sub-formation according to Prescott (1931), Beadle and Costin (1956), and Wood (1956)

Type	Dominant Tree Species	Prescott	Beadle & Costin	Wood
1	Tea Tree-Yellow Stringy Bark Bloodwood	DSF	DSF	LF
2	Blackbutt	DSF	DSF	DSF
3	Grey Gum	SW	Sh. W.	LW
4	Scribbly Gum-Yellow Stringy Bark Bloodwood	DSF	DSF (?)	LF/GF
5	Treeless	Heath	Heath	Heath
6	White Stringybark-Scribbly Gum Bloodwood	DSF	DSF (?)	LF/GF
7	Yellow Stringybark-Bloodwood	SW	DSF/SW	LF/GF
8	Apple	SW	Sh. W.	LW
9	Bloodwood	DSF	DSF (?)	LF/GF
10	Grey Ironbark	DSF	DSF	LF

Nomenclature of Species

Tea Tree	*Melaleuca leucadendron*, L. *sens. lat.*
Yellow Stringybark	*Eucalyptus acmenioides*, Shau
Red Bloodwood	*Eucalyptus intermedia*, R. T. Baker
Blackbutt	*Eucalyptus pilularis* Sm.
Grey Gum	*Eucalyptus seeana*, Maiden, var. *constricta*, Blakely
White Stringybark	*Eucalyptus phaeotricha*, Blakely & McKie
Scribbly Gum	*Eucalyptus micrantha*, D. C.
Grey Ironbark	*Eucalyptus drepanophylla*, F. Muell, ex Benth
Apple	*Angophora woodsiana*, F. M. Bail

Formations

DSF Dry Sclerophyll Forest
LF Layered Forest
GF Grassy Forest
LW Layered Woodland
SW Sclerophyll Woodland
ShW Shrub Woodland

The classification of the vegetation at the level of the Formation and sub-Formation according to the systems of Prescott (1931), Beadle & Costin (1952) and Wood (1956) is shown in Table I. At a finer level the original survey groupings have been transformed directly into 10 types which are also listed in Table I; this level of sub-division is analogous to the original partitioning. As used in this paper the word "type" does not denote an ecological class (*vide* Crocker and Wood, 1947) since the adoption of formal subjective units would accomplish nothing in this study; in common with the treatment of single species, it would require too much extrapolation from the original records, apart from vitiating their impartiality.

While the tree species vary, there is a very large common element in the understorys of the communities in the areas concerned. This is especially true of shrubs from the families Leguminosae, Proteaceae and Myrtaceae. The treeless type is normally a heath composed of many shrubs common in the understory of the forest communities, together with other epacridaceous and rutaceous shrub species and some sedges.

Results

A summary of the data is shown in Table II and the spatial distribution of soil phosphate within one area (Toolara A) is shown in Figure 2. The variability of soil phosphate within vegetal types seems obvious from inspection of the Table and Figure but statistical treatment certifies the disparities. By testing the differences between the means after weighting them inversely to their variances (Welch 1951) the vegetal types may be combined into homogeneous groups with respect to the mean total phosphate of the soils supporting them.

In Toolara A the vegetal types fall into two groups *viz.*—types 1-5 and 6-7; in Toolara B there are also two groups *viz.*—types 1, 3, 4, 6, 7, 8 and types 2 and 9; at Tuan Creek the groups are types 1, 3, 4, 5, 9 and types 8 and 10. While this grouping within areas suggests a degree of phosphatic control there is strong evidence to the contrary. In considering the data further the unplantable types are excluded due to the bias in sampling.

The two areas at Toolara are contiguous and almost identical in their combination of topography, soil and vegetation and, therefore, could be expected to give comparable results with regard to the common types if soil phosphate is the factor governing vegetal pattern. However, within Toolara A types 2 and 4 occur together in the lower phosphate group and types 6 and 7 in the higher

TABLE II. Summary of the results for the three areas concerned in this study. Results are expressed in parts per million of P_2O_5; P indicates plantable to *Pinus*, U, unplantable

TOOLARA A					TOOLARA B					TUAN CREEK				
Type	No. of Samples	Mean	S. D.	Range	Type	No. of Samples	Mean	S. D.	Range	Type	No. of Samples	Mean	S. D.	Range
1 U	22	69	43	20-206	7 p	8	56	27	21- 98	3 U	2	22	11	15- 30
2 p	46	78	33	20-180	3 U	2	69	1	68- 70	5 U	13	37	16	20- 80
3 U	34	82	45	14-212	4 p	118	70	34	21-192	1 U	15	43	14	15- 66
4 p	92	87	54	14-299	8 U	10	82	30	42-122	4 p	206	44	22	15-123
5 U	6	94	83	8-242	6 p	18	84	41	33-185	9 p	37	47	19	15- 88
6 p	79	115	68	20-315	1 U	2	92	21	77-106	8 U	3	53	6	47- 59
7 p	47	122	143	12-900	9 p	38	110	39	42-190	10 p	138	53	26	9-174
					2 p	3	121	53	64-169					

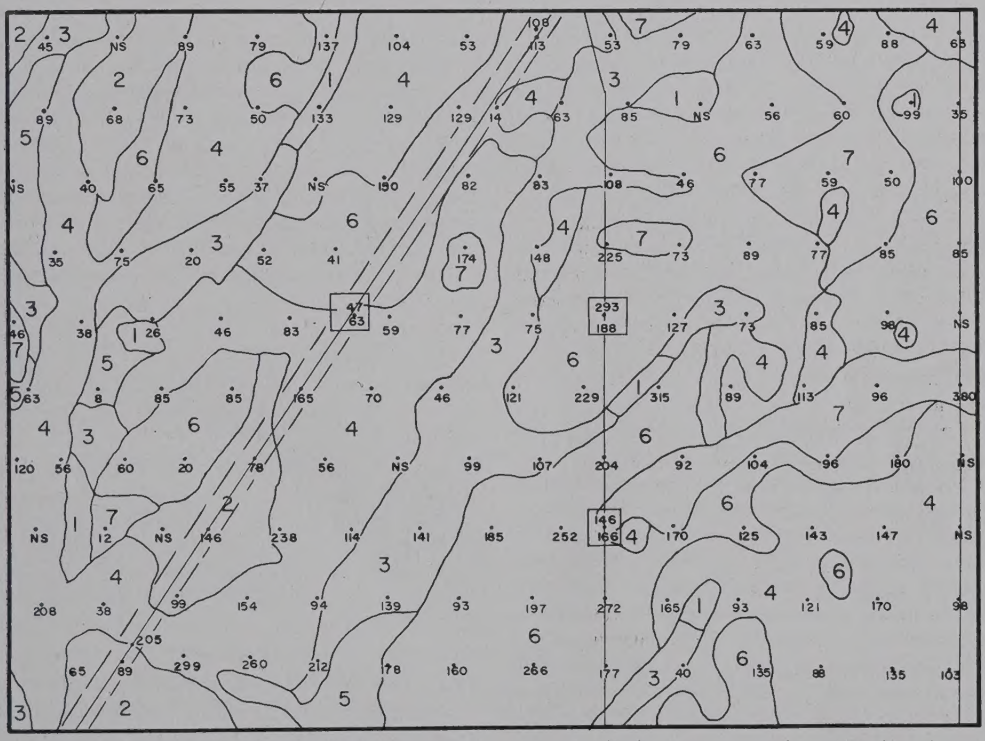

FIG. 2. Map showing the distribution of vegetal types and soil phosphate on portion of Toolara A area. Figures enclosed in a square represent samples collected at the end-points of different traverses but falling within 10 feet of each other. The continuous straight lines are survey base-lines; the broken lines indicate a surveyed roadway. Sampling points are on a 10 chain grid.

group; at Toolara B the position is reversed and types 6 and 7 occur in the lower group while type 2 is in the higher group; type 4 does not alter. Moreover, within Toolara A the mean phosphate for type 4 is significantly less than that for type 6 ($p < .01$) whereas in Toolara B they are not significantly different. Similar disparities seem to exist between types 2 and 6 and between types 2 and 7, but the paucity of data for these types precludes certainty.

Types 4 and 9 are significantly different at Toolara B ($p < .001$) but not at Tuan Creek. Finally, the restriction of Type 10 to Tuan Creek is also inconsistent with phosphatic control of distribution.

DISCUSSION

The conclusions drawn from this study apply only to the areas concerned but they should indicate trends which might be expected in similar country which extends unbroken from south of

Brisbane to North of Bundaberg, a distance of approximately 220 miles.

The results have to be interpreted with a degree of caution because chemical determination of total soil phosphate gives no clear indication of how much of this phosphate is available to the plant. However, the samples represent only the upper four inches of soil; here the chemical and physical factors governing availability of phosphorus are common throughout the areas. It may also be argued that the upper four inches represents only a portion of the root zone and that the soil phosphate could vary in the lower part. Experience with the soils of this region (for the soil groups concerned) indicates that the phosphate status of the surface horizon is a fair index for the rest of the profile. Examination of phosphate analyses on six soil profiles in the region indicates a positive correlation ($P = .01$) between total phosphate in the upper four inches and total phosphate in the upper part of the B horizon; these latter samples were from depths exceeding five feet. It seems reasonable to assume that although the argument rests on the upper four inches, the same relationships between distribution of vegetal types and phosphate will hold with regard to the rest of the root zone in these particular soils.

Allard (1942), Billings (1950), and Salisbury (1954) have reported cases in which soil phosphate was the initial limiting factor in the distribution of vegetation but these cases involved special circumstances in the local environment.

Beadle (1954) states that "for the communities of the Sydney district soil fertility is primarily responsible for the delineation of the various plant communities; soil phosphate is the factor which selects the vegetation with the possible exception of certain of the small patches of rainforest which may be climatically controlled." Moreover the title of Beadle's paper infers that this control is widespread in "Eastern Australia." By contrast, on this part of Coastal Queensland where the soils are generally low in total phosphate, there is a wide assemblage of communities and formations within which phosphate is not selective. Results from another region are given by Moore (1956) in a progress report on a study of factors governing the distribution of certain species of *Eucalyptus* on the Southern Tablelands of New South Wales. He states: "The work so far completed suggests that soil phosphate may be a factor of some importance in the distribution of *E. polyanthemos* and *E. melliodora*. However, it is clear from more recent work that other nutrients may be equally important, and that on the Southern Tablelands soil phosphorus cannot at present be regarded as playing a primary role in the distribution of communities, as concluded by Beadle (1954) for 'the Sydney district.'"

At the broader level of the Formation and sub-Formation on which Beadle bases much of his argument, it is also difficult to accept soil phosphate as the primary control for several reasons. Table II shows the overlap in range of soil phosphate under which the different Formations occur in the areas concerned in this paper. While the Formation is widely accepted as a structural entity there is still a conflict of ideas over its precise definition in Australia, which is exemplified by the contrast between the work of Prescott (1931), Beadle and Costin (1952) and Wood (1956) (Table I). A unit involving so much subjective judgment seems an unsuitable basis for the treatment of precise comparisons. Again the shrub layer in forests and woodland communities of eastern Queensland may be suppressed in favor of grasses for varying periods by intermittent fires. The consequent alteration in structure gives a different Formation and this fluctuation often occurs on a time-scale of less than 10 years; this is the case with types 4, 6, 7, and 9.

Under the prevailing conditions of low phosphate the type of vegetation at any point in this region results from the interaction of a large group of factors among which it is difficult to establish any single factor as the initial limitation. However, we do not wish to imply that phosphate could not be the controlling factor in other situations. These matters will be discussed elsewhere by Coaldrake.

From the variability of the original data, from the statistical results, and from the general arguments given above we conclude that soil phosphate does not determine vegetal pattern in the areas sampled.

Summary

Analyses of soil phosphate and records of native vegetation for 940 sites from three analogous areas in south-eastern Queensland have been examined statistically to test the hypothesis that soil phosphate is the primary factor governing the distribution of native vegetation in these areas. The results indicate that soil phosphate does not determine vegetal pattern in these areas irrespective of the level of classification of the vegtation.

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ROLE OF THE PLANT FACTOR IN THE PEDOGENIC FUNCTIONS

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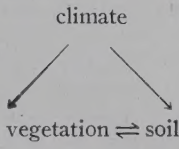
INTRODUCTION

The interplay of climate, soil, and vegetation is often represented by a triangle:



It implies that climate affects soil and vegetation independently, that soil influences vegetation, and that vegetation reacts upon soil.

While at first sight appealing the triangle is actually beset with logical pitfalls and frustrations. It has even led to the negativistic view that the soil-plant contract cannot be interpreted.

This paper presents a formalistic method for evaluating the various interactions. Assessing the roles of climate and vegetation in soil genesis will be emphasized. To do so, the concept of the biotic factor must be clearly delineated and given precision.

The writer follows a type of presentation which he has offered for a number of years to his students in pedology. It is fair to say that both Major and Crocker attended these lectures, prior to their own pertinent publications (Major 1951, Crocker 1952). In turn the writer has profited from their considerations.

THE TESSERA AND THE LARGER SYSTEM

In a given landscape let us select a spot, say, an area of one square meter, or a square of 8 x 8 inches, or any other small area of suitable shape. There is soil with organisms below it, and there is plant and animal life above it. The totality constitutes a three dimensional element of landscape, an arbitrary element. The element is an open system; matter is continually added to and removed from it.

The entire landscape can be visualized as being composed of such small landscape elements. This picture is comparable to the elaborate mosaic designs on the walls of Byzantine churches which are made up of little cubes or dice or prisms, called tesseras. We shall use the same name, tessera, for a small landscape element.

The "thickness" of a tessera is given by the height of vegetation plus the depth of the soil. The area of a tessera is determined by operational considerations. It is a convenient sampling unit having a specified area. A quadrat or rectangle of one square meter in a stand of vegetation is a vegetation tessera. A soil monolith is a soil tessera. A "soil profile" collected in the field is a soil tessera, usually of ill-defined areal dimensions. Strictly speaking, a soil profile is a vertical face of a soil tessera.

Table I illustrates the total nitrogen assay, by Kjeldahl analysis, of an alpine tessera collected in 1955 on a 315-year old moraine in front of the Rhoneglacier in Switzerland. The vegetation was alpine shrub, consisting mainly of *Rhododendron ferrugineum, Vaccinium myrtillus* and *Juniperus nana*.

On the ground a square of 400 sq. cm. was marked off. Plants were clipped along the upward vertical projection of the square, then cut at the base, dried, weighed, ground up, and analysed. Soil layers were carefully collected along

TABLE I. Nitrogen assay of an alpine shrub tessera, 315 years old

Description of layer or horizon	Thickness of layers, cm	Grams of nitrogen in layers of 1 sq. m. area
Vegetation	23	25.0
Litter layer	0 - 2.5	43.8
Humus horizon	2.5 - 9	67.8
Light gray horizon	9 - 20	5.9
Brownish horizon	20 - 34	37.3
Brownish gray horizon	34 - 60	16.9
Dark gray horizon	60 - 95	27.4
Dark gray horizon	95 - 100	0.0
	123	224.1

the downward vertical projection of the square. Each layer was weighed, roots were picked out, and all parts were analysed separately. Nothing was discarded.

Note that the boundary between vegetation and soil is wholly arbitrary. It cannot be otherwise, as it is impossible to separate quantitatively the mineral soil fraction from rootlets, roothairs, insects, microbes, not to mention the separation of living and dead materials. The base of the vegetation layer was set at the upper plane of the litter layer. Everything below it, dead or alive, was classified as soil. Since interest centers on the tessera as a whole the arbitrariness of its subdivisions is of minor concern. The total nitrogen content of the tessera is 224.1 g/sq. m. or 2000 lbs/acre. Accordingly, the average annual net gain was 6.35 lbs of nitrogen per acre. The portion in the vegetation layer amounts to 11 per cent only. The horizon values include the portions in the roots picked out. They contributed 4.6 per cent of the total system value.

Mosaics of tesseras, from at least two to many millions, are designated as larger systems. Like tesseras, the larger system constitutes an ensemble of soil, plant life, animal life, including man. In this respect it is akin to the ecosystem of Tansley, or the biochore of Pallmann; but, its areal extent is entirely arbitrary. One may also say that a tessera, which is a small system itself, is a larger-system element, or an ecosystem element, or a biochore element. As mentioned before, it is also a landscape element.

We place stress on tesseras because they are the concrete working units in field research. They are the "samples" in statistical calculations. For instance, the average composition of a larger system is obtained by statistical treatment of randomized tesseras having equal areas. Pedogenic functions are arrays of soil tesseras.

Any specific property of the tessera and the larger system is denoted by 1 (from the first letter of landscape), any individual soil property by s. Vegetation properties, such as quantity of growth, number of species, frequency of species, are given the symbol v. In Table I, for nitrogen, $1 = v + s$, or, $224.1 = 25.0 + 199.1$. In general, however, there is not necessarily a simple relationship between quality and quantity of l, v, and s. Moreover, animal life also should be recognized explicitly.

We postulate the following definitions of the state of the larger system and the tessera and its subdivisions, vegetation and soil:

Larger system,
tessera: $l = f_l\ (cl, o, r, i, t)$ (1)
Vegetation part: $v = f_v\ (cl, o, r, i, t)$ (2)
Soil part: $s = f_s\ (cl, o, r, i, t)$ (3)
or, abbreviated, $l, v, s, = f\ (cl, o, r, i, t)$ (4)

The letters in parenthesis signify climate (cl), the biotic factor (o), topography (r), time (t), and the initial state (i) of the system as far as l-, v-, or s-properties are concerned. These five factors are identical with the soil forming factors or soil formers or pedogenic factors of the pedologist; i usually is equal to p, the parent material. Since the word "formers" may suggest a notion of causality or mechanism, which is not implied, we prefer to use here the expression "state factors." All system properties, l, v, s, are considered dependent variables, being dependent on the state factors.

The four equations indicate that any property of the system and its parts is fixed, conditioned, determined, if specific magnitudes are assigned to the state factors listed in parenthesis. The above equations are generalizations based on countless observations made by pedologists and ecologists.

THE FIVE PRINCIPAL GROUPS OF SYSTEM FUNCTIONS

So far, nothing has been said that is not known to any naturalist. The point of departure is the belief that the definition equations can be shaped into a sharp tool for field research in pedology, ecology and certain aspects of geomorphology. To accomplish this, the state factors cl, o, r, i, t are given the status of independent variables; that is, they are not supposed to be related to each other. This is a limitation placed on the four equations which restricts their generality. Yet, it is this very restriction that renders the equations useful for research in such areas where the state factors do vary independently of each other.

We now expand the well known function of soil forming factors (Jenny 1941) to include the

tesseras. We arrive at five groups of tessera functions or even larger-system functions:

$l, v, s = f_{cl}(cl)_{o,r,i,t}$	climofunctions
$l, v, s = f_{o}(o)_{cl,r,i,t}$	biofunctions
$l, v, s = f_{r}(r)_{cl,o,i,t}$	topofunctions
$l, v, s = f_{i}(i)_{cl,o,r,t}$	lithofunctions
$l, v, s = f_{t}(t)_{cl,o,r,i}$	chronofunctions

The solution consists of evaluating "f," that is, the kind of dependency the properties l, v, s, display when only one state factor varies and the others remain constant.

In nature this may be accomplished in two ways. First, by the overall statistical approach, by collecting a vast number of tesseras at random and then correlating their properties with the state factors. Second, by abandoning overall random sampling and substituting directional random sampling in accordance with the five functions. This approach produces good functions with fewer tesseras. In either case it is not necessary that the factors "held constant" are actually held constant as long as their variation does not affect the dependent variables l, v, s (Jenny 1946).

When the variables are expressed qualitatively instead of quantitatively we speak of sequences rather than functions, e.g. sequences of tesseras and larger systems, sequences of soil types or sequences of plant communities.

The state factors must be so defined that they can vary independently of each other:

cl denotes the climate measured above soil and vegetation. This climate of the "surrounding" is sometimes called regional climate. The climate at any point inside the tessera, the internal climate, is cl'. Depending on where it is measured the internal climate is known as microclimate, Klima der bodennahen Luftschicht, soil climate, etc. In the factorial approach cl' is always treated as a dependent variable, being dependent on cl, o, r, i, t. Thus, the moisture regime of a soil varies with soil age, whereas precipitation does not.

o is the biotic factor, restricted in the present paper mainly to plants. It is the purpose of this discussion to delineate the independent and dependent aspects of the plant factor.

r represents the group of factors that make up topography, particularly in the initial state. The geologic ground water table (Jenny 1946) is also an independent variable and is here grouped with r.

i is the initial state of the system and its parts. If vegetation is absent or negligible at the start of system development, i becomes equal to p, the parent material concept of the pedologist.

t is the time of development or age of the tessera or the larger system. t_o is time zero, the starting point, chosen arbitrarily on the infinite time scale of system evolution.

In view of these definitions it is clear that the state factor approach chosen differs in principle from the holocoenotic concept of plant environment (Billings 1952) because of its accent on dependent and independent variables and because it does not concern itself with relations among state factors.

Models and Imaginary Experiments

The understanding of nature is our ultimate goal. It does not follow, however, that analysis of natural soils and vegetation constitutes the exclusive approach. Much can be and is being learned from experimental studies of system development, though this phase of research is still in its infancy (Knapp 1954).

The experimental approach is particularly helpful for examining the role of the plant factor in system development. We shall set up models and imaginary experiments. Although they deviate from natural systems by an uncomfortable margin, these over-simplifications are most helpful in clarifying the independent and dependent aspects of the biotic factor and allied conceptual questions of system analysis. We shall group our inquiry around the five principal functions, though, for pedagogic reasons, not in the order given above.

Analysis of Biofunction and Biosequence

To assess the role of the plant kingdom as a state factor we must solve the equation

$$l, v, s = f_{o}(o)_{cl,r,p,t}$$

The plant biotic factor "o" appears as an independent variable, whereas the other state factors are held constant. The question as to what is actually implied by designating "o" as an independent variable will now be answered by several imaginary experiments which have a direct bearing on problems encountered in the field.

Experiments with annual plants

We visualize three large tanks filled uniformly with loess material. The surface is made level. The tanks are placed into three separate, large growth chambers with elaborate climate control, so-called phytotrons. A humid climate is chosen, the same for all three tanks. Tank No. 1 is left bare; tank No. 2 is seeded to a grass species; to tank No. 3 is added inoculated legume seed. The plants are harvested prior to seed setting and the tanks are reseeded again. This procedure is continued for 50 years.

A sketch of the experimental design is shown in Figure 1. The constellation of the state factors is as follows:

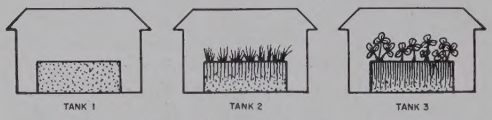


FIG. 1. Experiment with annual plants (grass, legume) to isolate the biotic factor. Each tank is a "larger system."

Factors	*Tank No. 1*	*Tank No. 2*	*Tank No. 3*
o	zero (*bare*)	*grass*	*legume*
cl	humid	humid	humid
r	level	level	level
p	loess material	loess material	loess material
t	50 years	50 years	50 years

Only "o" differs, all other factors are identical, viz. constant.

At the end of 50 years the three identical parent materials will have developed into three different soils. Owing to symbiotic nitrogen fixation the legume-tank is likely to be higher in nitrogen and organic matter than either the bare tank or the grass tank. Yield and composition of plants also are dissimilar. Since cl, r, p, t are invariant, the differences in soil and vegetative properties are exclusively the consequence of the different species introduced. They, their genotypes, are the two different biotic factors. They are "independent" in the sense that their selection and addition had not been influenced by the original choice of cl, r, p, t. The seeds originated "outside of the system."

The soil differences between Tank No. 1 and Tank No. 2 are attributable to grass; the differences between Tank No. 1 and Tank No. 3 to inoculated legume; the differences between Tank No. 2 and Tank No. 3 reflect the differences in the biotic factors grass versus legume. These two tanks constitute a biosequence.

Had we imposed other conditions of parent material and climate, but retained the grass and legume germules, soil and vegetative properties between tanks No. 2 and No. 3 would again differ; also, they would differ from the experiment chosen. Nevertheless, we would again attribute soil variation to species variation. The species is the independent biotic factor, not the amount of growth which is a dependent variable.

It may be well to note that state-factor analysis is not concerned with processes, that is, questions of molecular, ionic, colloidal, biochemical, enzymatic mechanisms that produce different soils. The approach is strictly descriptive, formalistic. Its aim is to evaluate the dependencies of l, v, s on cl, o, r, i, t.

Experiment with pure stands of perennial species

We enlarge two tanks to permit tree culture. One tank is planted to oaks, the other to pines (Fig. 2). We do not disturb the trees. At the end of 100 years we examine the two tanks. The soils have different A_o and A_1 horizons. We have an oak-soil and a pine-soil since all factors other than species are identical. The two species are the two biotic factors.

FIG. 2. Experiment with pure stands of oaks and pines. Soil differences correspond to species differences.

Experiments with mixed stands of perennial species

We operate with the same loessial parent materials. Into tank No. 1 we insert a germule mixture consisting of ten per cent oak and ninety per cent pine seeds. To tank No. 2 we add the reverse proportion, ninety per cent oak, ten per cent pine seed. We reseed annually, but do not cut the trees (Fig. 3).

FIG. 3. Experiment with mixed stands of oaks and pines. The white and the dashed bands are tesseras which approach the conditions of tanks 1 and 2 of Figure 2.

In a few years, prior to natural seed production, the bulk composition of the soils in the two tanks will slightly but measurably differ, owing to the species frequencies. In each tank the biotic factor is the sum of the species, oak and pine, *plus their frequencies.*

If the two mixed-culture tanks are left to themselves for many centuries their stands and proportions of species will become more and more alike. Although we keep adding annually the original seed mixture the total seed population in the tanks will become slowly modified in the direction of identity. The total seed population falling on the soil in either tank is $(\text{seeds})_{\text{outs.}} + (\text{seeds})_{\text{ins.}}$, the seeds added from the outside, a constant quantity, plus the seeds produced inside the system, a variable, time-dependent quantity. The sum $(\text{seeds})_{\text{outs.}} + (\text{seeds})_{\text{ins.}}$ is thus also a

function of time. Therefore, seed frequency is no longer a component of the biotic factor.

The frequency factor of the initial germule is the more influential the longer the life spans of the species involved.

Such tank experiments with trees are actually being conducted by the United States Forest Service at San Dimas, California.

Instead of analysing the two tanks *in toto* we might wish to collect soil tesseras under oaks and compare them with soil tesseras under pines. These two groups of tesseras would permit evaluating the species effects, similar, though not identical, to the experiment with pure stands of perennials.

This is exactly what is done in practice in forests where species are randomized or had been planted by man according to some preconceived geometric pattern. Müller (1887) long ago attributed podsol to heath, brown forest soil to oak. Very striking effects are observed in New Zealand where giant podsol occurs under Kauri pine, and, a few feet away, black soil under other species. These soil comparisons mirror biosequences.

New system cycle

If we cut the forest of one of the two tanks in the preceding experiment and replant it to an entirely new set of species, a new development cycle is instigated. It may then be convenient to start counting again. The soil S becomes S^o, the parent material of a new, future soil. But, note that the new set of species was introduced from the "outside," producing a change in o. Vegetational changes resulting from plant succession under constant o do not fall into this category of "new system cycle."

Flora plus fauna and man

Two huge tanks of several acres in area are sprayed annually with seed mixture containing forest trees and grass species. After a while man enters one of the tanks and lives on it permanently. He interferes with plant growth through burning, cutting of trees, etc. The two larger systems may be considered as having two different biotic factors, *trees* + *grasses* in tank 1, *trees* + *grasses* + *man* in tank 2. Instead of man a grazing animal, e.g., bison, might occupy tank No. 2 and maintain grassy areas in accordance with population pressure. The biotic factor would then consist of *trees* + *grasses* + *bison*.

Interaction of two larger systems

In a large phytotron are two soil tanks, separated form each other by a partition which prevents transfer of matter. Tank No. 1 has a dense grass sod; tank No. 2 carries a eucalyptus grove (Fig. 4). All other state factors, cl, r, p, t, are identical. We have two separate larger systems, Lg and Le, the soil differences having been produced by the two different floras. The two systems are members of a biosequence.

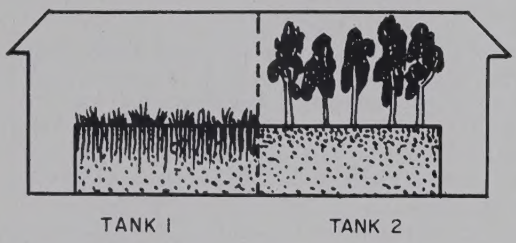


FIG. 4. Interaction experiment with two larger systems, grass and eucalyptus.

In nature the partition may result from mechanisms of seed distribution.

We remove the partition and bring the two tanks into contact. Interaction becomes possible. Let us examine it carefully.

There is now but one biotic factor for both tanks, grasses + eucalyptus, because germules have access to either tank. Since each tank acquired a new biotic factor the two larger systems Lg and Le become Lg^o and Le^o, the initial states of a new cycle of system development. Given sufficient time the new systems will blend in some fashion. Until they become identical, which may or may not happen, the two new systems will continue to form a true biosequence, not because of a difference in the present biotic factor, but, because of the different initial states, Lg^o, Le^o, which differed only in o, not in cl, r, p, t.

Judging from actual experience in California, eucalyptus will move slowly into grass, along a narrow fringe, in which the grassland soil—now a parent material—is transformed into a new soil which, however, is not necessarily identical with the original eucalyptus soil; it is, in European terminology, a "degraded" grassland soil.

As may be surmised, the "interaction" experiment and the "flora-fauna-man" experiment allude to the crucial pedological and ecological problem of the prairie-timber transition zone (Smith et al. 1950). The "flora + man" and the "flora + fauna" set-ups correspond to the hypothesis which attributes the creation of grasslands in forest areas to Indian fires or grazing bison. The "interaction model" describes the conditions as they exist today, the grassland persisting but slowly giving way to forest. From the viewpoint of factorial analysis it does not matter in what manner the two tanks (two integral systems) are brought into interacting juxtaposition, whether by grazing,

burning, or change in climate. These interesting questions are outside of its realm.

Analysis of Lithofunction and Lithosequence

In the lithofunction

$$l, v, s = f_p(p)_{cl,o,r,t}$$

parent material appears as the variable factor whereas "o," is invariable, or "constant." We shall inquire about the meaning of a "constant biotic factor." As pointed out, when a system starts with a mineral matrix devoid of vegetation we write p rather than i, to follow pedologic use of symbols.

We resort again to two tanks in two phytotrons. This time they are filled with different parent materials, crushed serpentine rock in tank No. 1, and loess material in tank No. 2. Both tanks are seeded to identical mixtures of perennial grasses and inoculated legume species. We shall not harvest. The constellation of the factors is as follows:

	Tank No. 1	*Tank No. 2*
climate (cl)	humid	humid
biotic factor (o)	grasses + legumes	grasses + legumes
topography (r)	level	level
parent material (p)	*serpentine*	*loess*
time (t)	100 years	100 years

A century of development will produce two different types of vegetation and soil. Owing to an unfavorable Ca:Mg ratio and possibly a molybdenum deficiency plant production on serpentine will be greatly inferior compared to growth on loess. The loess soil will be richer in humus and will have more profile development than the serpentine soil. The two systems are members of a lithosequence (Fig. 5), having a constant biotic factor, the grass and legume species.

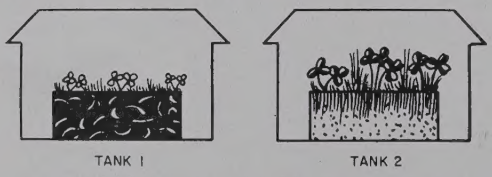


Fig. 5. Lithosequence of larger systems, comparing serpentine rock in tank 1 with loess material in tank 2.

Contrary to common pedological parlance we would *not* say that the higher humus content of the loess soil is the result of its more luxurious vegetation, for, with equal justification, the ecologist could claim that the abundant vegetation is caused by humus-rich soil. To avoid circular reasoning, factorial analysis demands that we attribute all soil and vegetation differences in tanks 1 and 2 to the variation in parent material.

But, suppose we harvest at the end of the century and replant identical species, e.g., oats, on each tank. Then the two soils assume the role of parent materials. The oat yield differences obtained reflect the fertility of the two "soils."

Turning to natural systems, Curtis (1955) has recently produced for Wisconsin prairies numerous continuous functions between "presence percentage of species" and water retaining capacity of soils. If the latter is conditioned by texture of parent material, as seems very likely, his curves are typical lithofunctions of species distribution.

Yang and Lowe (1956) in Arizona compared two major climax vegetations on unconsolidated desert alluvium, so-called fanglomerate. The Paloverde-Sahuaro vegetation type occupies the higher rocky slopes, whereas the lower slopes with finer textured material support the Creosote bush-Bur Sage association. Between the two associatins is a broad area of ecotone where one distinct vegetation type first merges and then gives way to the other. Since topographic features and macroclimate are uniform over the entire area, the two associations and their transitions represent a typical lithosequence of vegetation, more specifically a parent material texture sequence. One would expect soil properties to vary in corresponding fashion.

Analysis of Topofunction and Toposequence

We wish to study vegetation and soil in relation to topography in accordance with the equation

$$l, v, s = f_r(r)_{cl,o,p,t}$$

Relief is the only variable state factor, all others, including the biotic factor, are constant.

We choose a very large tank, some 20 feet deep and a hundred feet long. It is filled with wind blown material of sand and silt size in such manner as to form two ridges and a trough. The vessel is inserted into a large phytotron which simulates a dry climate and maintains a salty water table near the surface of the trough (Fig. 6).

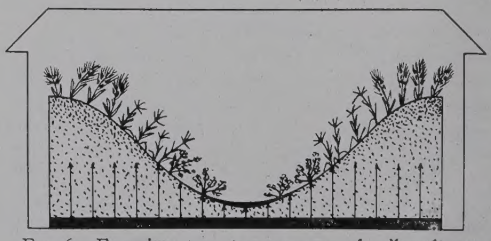


Fig. 6. Experiment on toposequence of soil and vegetation. Black area at bottom of tank indicates salty water table; arrows denote capillary rise of salt water Black area in trough is a playa.

Annually a specific seed mixture is applied, consisting of highly salt tolerant halophyte plants (e.g. *Atriplex cordulata*), medium salt tolerant species (e.g. Bermuda grass), and salt intolerant species (e.g. *Bromus rigidus*).

A few centuries will suffice to delineate characteristic soil and vegetation patterns. In analogy with field conditions we would expect high salt accumulation in the trough (saline soil) which prevents the seeds from germinating. The ridges are salt-free, carry brome grass predominantly and have soils approaching the well drained, regional upland-type. On the slopes the salt content of the soil increases from ridge to trough in proportion to capillary rise. The halophytes are near the bottom and the less tolerant species are arranged along the slope in relation to their salt tolerance. We have a characteristic topofunction of soil and vegetation.

The biotic factor of any segment of the transect, that is of a strip along the contour, is given by the sum of all the species, the flora of the tank. The actual distribution of the plants along the slopes is a strictly dependent phenomenon. While the frequency of the species in the initial seed population might have been pertinent in the early stages, and thus constituted part of the biotic factor, it soon became a slope-dependent variable in accordance with the arrangement of the growing species.

Note that the playa in the trough, though bare of vegetation, still possesses the same biotic factor as any other slope portion. Specimens of seeds of all species in the system reach it. The biotic factor of any segment is its potential flora.

Contrary to the experiment with mixed stands of perennials, one cannot isolate the species factor in soil formation. Although soil under Atriplex differs from soil under Bromus this soil variation cannot be attributed to species since their distribution is not randomized. It is itself related to slope and distance to water table.

Actual tank experiments on the influence of depth of water table on plant competition have been conducted by Ellenberg (1954). Elgabaly (1954) has published a slope sequence of soil and vegetation on sand dunes near El Arish, Egypt, which is similar to our model. The dune is quite uniform in texture and calcium carbonate content and differs only in salt content, mainly sodium chloride and sulfate, in accordance with the plumb distance from the dune surface to the salty water table. Figure 7 shows the position of the dominant plant species and the corresponding total salt content of the soil, in per cent, to a depth of 25 cm. In the saline trough there is no growth; the ridge is nearly free of salt.

Very recently Russell and Rhoades (1956) in Nebraska have analysed in detail a toposequence with a strong water-table component. Slopes and curvatures as they affect soil nitrogen have been studied by Aandahl (1948). Tüxen (1954) reported on the distribution of forest associations in relation to topographic features.

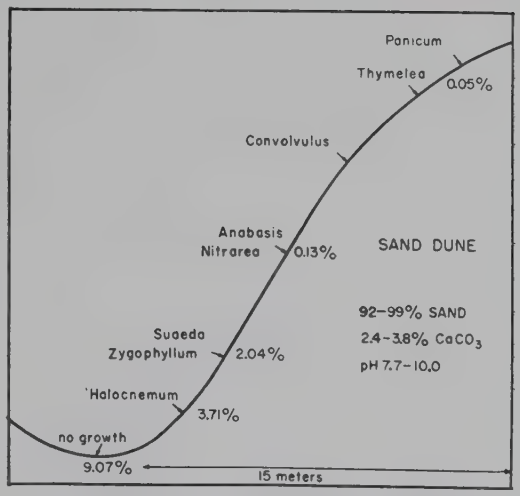


FIG. 7. Elgabaly's toposequence on saline, calcareous sand in Egypt. Percentage figures along slope denote salt content. In the bottom of the trough, soil texture is somewhat finer, 75 per cent sand. The height of the dune is 13 meters.

EXAMPLE OF CLIMOFUNCTION AND CLIMOSEQUENCE

The formulation

$$l, v, s = f_{cl}(cl)_{o,r,p,t}$$

relates the properties of tesseras and larger systems to climate, under constancy of all remaining factors. Here, the idea of a "constant biotic factor" is most frequently misunderstood. How could the biotic factor be held constant in view of the responsiveness of vegetation to climatic variations?

We select a tank of enormous proportions, 20 feet deep, hundreds of feet wide, and many miles long. It is filled uniformly with calcareous material. The colossal phytotron needed for this test is so ingeniously constructed as to be able to produce a horizontal rainfall gradient. On the one end of the tank the climate is arid, at the other it is humid (Fig. 8). This particular arrangement simulates a narrow strip of land extending from the Nevada desert to the Atlantic Coast, along a line of constant mean annual temperature.

With special instrumentation we shall insert, annually and uniformly over the entire area, the potential vegetation in the form of a seed mixture consisting of such species as (1) sagebrush, (2) buffalo grass, (3) wire grass, (4) bluestem grass, (5) oaks, (6) pines, and (7) firs.

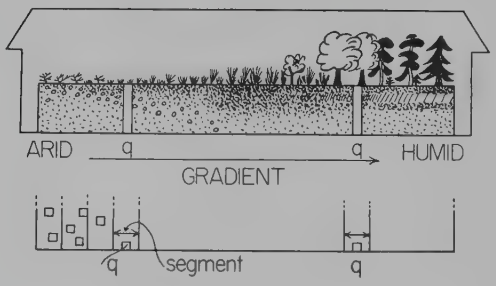


FIG. 8. Large-scale experiment on climosequence with uniform moisture gradient from arid to humid climate. The letters q denote soil tesseras.

Within a century or two a distinctive carpet of vegetation will have been established, and soil differentiation will be observable. In analogy with natural vegetation in the United States, sagebrush would be expected to occupy the desert area, buffalo grass and wire grass the semiarid sector, and bluestem the semihumid one. The tree species would tend to cluster in the humid end of the tank. The soils would represent initial stages of sierozem, chestnut soils, chernozem, prairie soil, podzolic soils.

Had we introduced an entirely foreign biotic factor, such as an assortment of Australian species, the soil sequence might be markedly different.

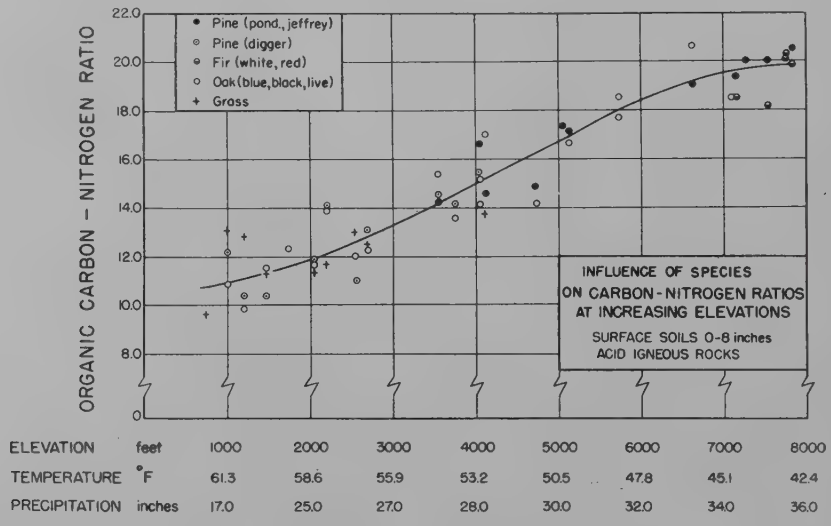
The distribution of the species and their quantity of growth is strictly a moisture dependent variable, and so is the germule frequency which is made up of the portion we add from the outside of the system and the amounts produced within the system.

To assess the biotic factor we divide the giant tank into a series of climatic segments, strips, or sub-tanks at right angles to the moisture gradient. In Figure 8 the lower graph provides a bird's-eye view of the segments, each having within itself a uniform climate. Each sub-tank may be compared to the experiment with mixed stands of perennials.

The biotic factor of any segment of the transect is simply the sum of all the species in the entire tank. It is "constant" in the sense that seeds of all species reach all parts of the system at suitable time intervals. It is legitimate to collect tesseras (q in Figure 8) throughout the tank and plot their mean analytical values for segments in relation to rainfall, and thus solve the climofunction.

But, it would *not* be proper to claim that the soils in the humid end of the tank are acid because they are covered with coniferous trees, or, in the arid end, that sage brush grows because the soils are calcareous. Throughout the tank both soil and vegetation are simultaneously conditioned by climate. To say that one dependent variable is the cause of another dependent variable leads to logical entanglements that create no insight.

However, it is correct to compare soils under two different species and isolate the species factor on soil genesis, provided the species grow at the same rainfall; for, at right angles to the moisture gradient the species pattern is randomized and cl, r, p, t are constant. The situation corre-



ELEVATION	feet	1000	2000	3000	4000	5000	6000	7000	8000
TEMPERATURE	°F	61.3	58.6	55.9	53.2	50.5	47.8	45.1	42.4
PRECIPITATION	inches	17.0	25.0	27.0	28.0	30.0	32.0	34.0	36.0

FIG. 9. Climofunction in the Sierra Nevada showing the C/N ratio of soils in relation to elevation and to kinds of species.

sponds to the experiment with mixed stands of perennials.

Pertinent soil and vegetation climofunctions and sequences have been published by many investigators (Jenny 1941, Dansereau 1956). The impressive moisture transect of Whittaker (1956) in the Great Smoky Mountains is, however, a questionable one since the complex moisture gradient chosen appears to refer to cl′ rather than cl.

A climofunction that is in accord with the ideas advanced is shown in Figure 9. It relates the carbon-nitrogen ratios of surface soils to elevation (Harradine and Jenny 1957). Soil samples, to a depth of eight inches, and six feet from tree trunks, were collected on the west slope of the Sierra Nevada in California. Parent material was restricted to granitic rocks; topography was held constant to the extent that only south-east exposures, having slopes between 16 and 32 per cent, were sampled. Since in this region soil organic matter appears to be in a steady state condition, time variation has a negligible effect. Only vegetation and climate vary, both in accordance with elevation.

The curve, free-hand drawn, connects the average C/N ratios of successive climate segments (elevation segments). It is a climofunction. The plus and minus deviations from the line record the species effects on the soil organic matter, the biosequences. They are, in this particular transect, of minor importance compared to the strong climatic component.

The justification for attributing the low C/N ratios at low elevation and the high C/N ratios at high elevation to differences in the climates of the two sites rather than differences in their floras lies in the observation that species distribution is itself a function of climate. It implies that there are no physical barriers to germule migration.

Analysis of Chronofunction and Chronosequence

The equation

$$l, v, s = f_t(t)_{cl,o,r,p}$$

deals with soil and vegetation development in a constant climate and with a constant biotic factor.

If one simply writes

$$l, v, s = f(t)$$

without subscripts, the formulation portrays the strictly historical approach: a landscape element is being observed and studied during hundreds and thousands of years, regardless of changes in cl, o, r. The pure chronofunction, on the other hand, is restricted to such time periods that satisfy the conditions of constraint of the state factors. In particular, there are thus the following two kinds of plant successions: those taking place at constant o, and those occurring under conditions of variable o.

Let us fill a tank with fine igneous rock material and place it in a cold, humid climate. A mixture of seed is added annually ("constant o") consisting of calciphile legumes, and grasses, herbs, calluna and vaccinium. Such an arrangement is approximated by morainic material in a high alpine mountain valley, above the timber line, where the same kinds of seeds are annually blown in from surrounding areas.

All species grow. The initial vegetation mosaic is randomized in accordance with seed incidence. As soil formation advances the basic rock constituents are leached out and raw humus accumulates. The calciphile legumes succumb and the acid tolerant shrub species become dominant. While the biotic factor is still the sum of the species that reach the area, and thus is invariant, the vegetation observable differs radically from it since the legume species have ceased growing. Clearly, the actual flora is no longer the biotic factor.

The situation is portrayed in Figure 10, with time of soil formation on the horizontal axis, soil nitrogen on the vertical. The maximum of the curve is meant to coincide with the disappearance of the legumes. A new, lower level of nitrogen stabilization is being striven for, possibly the same one that would have been achieved had the biotic factor never included the legume component (dotted line).

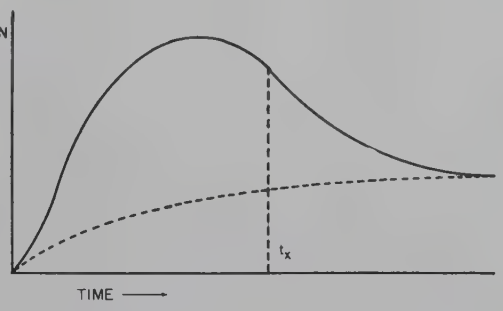


Fig. 10. Illustration of chronofunction of soil nitrogen. Solid curve: accumulation of nitrogen in presence of legumes, and its depletion after elimination of legumes. Dashed curve: nitrogen accumulation in absence of legume component.

At t_x the system is not defined by enumerating the species growing in the tank. The total plant disseminule has to be taken into account since the vanished legumes still leave their impress on the soil.

An excellent chronofunction of soil and vegetation has been published by Dickson and Crocker

(1953/54). Size of lichen patches on rocks dated from 1600 to 1955 have been correlated as time functions by Beschel (1957).

Recapitulation of the Concept of the Biotic Factor

In the experiments discussed the plant cover is divided into flora and vegetation. Flora refers to kinds of species in a chosen landscape, regardless of the number of individuals of each species. Accordingly, the flora of an area or system is given by a species list. It may contain but one entry (experiments with annuals and pure stands of perennials). Vegetation, on the other hand, pertains to quantity and quality of growth. It is always a dependent variable, being dependent on cl, o, r, p, t of the system under consideration.

For the sake of clarity let us designate the germule, the kinds of species that reach a given barren area from the "outside," as φ_1, φ_2, φ_3, . . . , in general as φ. These germule species constitute the plant-biotic factor φ of the general biotic factor o. They are the potential flora of the area. The species which actually grow in the area are f_1, f_2, f_3, . . . , in brief, f. Like vegetation, f is a dependent variable.

In the experiments with annual plants, pure and mixed stands of perennial species, and lithofunction, the two floras φ and f of the entire tank are identical. They are also identical for segments or sub-tanks of suitable size. Accordingly, the biotic factor is the sum of the species growing in the tank or in its segments.

In a second group of experiments, the topofunction and the climofunction, the actual flora of the entire tank is also equal to the potential flora, the biotic factor, but, for individual segments φ and f differ. The biotic factor of any segment is the sum of the species growing in all segments.

In a third type of experiment, the chronofunction, the actual flora f at time t_x is not equal to φ. The biotic factor of the tank cannot be deduced from examination of the species growing at time t_x, since some species that reach the area no longer survive.

Evaluating the Biotic Factor in Nature

The imaginary experiments are helpful in clarifying the concept of the biotic factor. They serve as guides for assessing real systems. In the field it is extremely difficult to measure the precise plant diaspore, φ. One would have to collect the entire disseminule that reaches a selected area during its development cycle.

As a substitute for this true biotic factor the writer proposes a first approximation.

The species growing within the chosen area at time t_x constitute the actual flora, f. It is, however, only part of the biotic factor φ, the growing part. The remaining part comprises all those species which enter the area under consideration, but which are not growing at time t_x.

This unknown part may be estimated from the aggregate of species living in the region surrounding the area under consideration. The extent of the region is circumscribed by the dispersal capacity of the species, which is conditioned by the nature of the germule and the dispersion barriers.

The floral list which includes the actual species of the system and those living in the surrounding areas is a first approximation to the true total biotic factor; it is the *minimum biotic factor* of the system selected. Generally speaking, only those tesseras which have the same minimum biotic factor can be arranged into cl, r, p, t functions or sequences.

Crocker (1952) has presented a searching and illuminating analysis of certain aspects of the biotic factor. He narrowed the definition of the biotic factor by eliminating from the floral list all those species which have not yet grown at time t_x. This partial floral list Crocker designates as the effective disseminule factor.

Crocker does not tell us how we are to determine in the field the effectiveness of a germule. Surely, not by its growth only. Its mere presence may act as a stimulant or deterrent to the growth of other species by furnishing crucial components such as organic substances or missing micronutrients. Nor is it clear how the lost developmental flora of a tessera could be ascertained. Most important, all these considerations pertain to growth, which is conditioned by the constellation of the state factors. Following Crocker's definition, we could not solve pedogenic functions, such as the climofunction of Figure 9, since each segment would have a different effective biotic factor, and thus "o" could not be kept "constant." Likewise, the playa in Figure 6 would have a zero biotic factor, according to Crocker, since it has no "ecosystem-suited flora." The playa could not be considered an integral part of the toposequence. In our opinion there is a crucial difference in state factors between the bare playa of Figure 6 and the bare tank in Figure 1, and this difference rests in the biotic factor.

Sjörs (1955) also objects to Crocker's position. He goes a step further and denies that the organism factor is, or ever was, independent of the ecosystem, "If we turn to past ages, there is fair evidence that organisms and environments have always been interrelated within ecosystems."

The writer contends that in nature sites and regions are available in which the potential flora

is independent of the site or region itself. Classic examples are provided by land freed from glaciers, or land covered by volcanic ash (e.g. Krakatau) and by flood sediments. The disseminule reaching these areas is genetically independent of the area itself. If subsequently species evolution occurs within the area, the new products are dependent variables. It is exactly such specific sites and regions that lend themselves to functional analysis. Crocker, forseeing Sjörs' objection, succinctly stated: (1952 p. 151) "The regional flora can be considered independent because the basic segregation (of general flora) into regional flora preceded soil-formation time zero." It all depends when we start counting, that is, what system state we select as L^o.

Polyfunctions and Polysequences

The five principal functions, important as they are for ecosystem research, are not easily observed in nature's mosaic display of factor combinations. One has to search for them deliberately, seek them out.

Rather frequent are functions of combinations of two or more factors. Along a mountain slope precipitation increases with elevation, temperature decreases. The two factors are confounded. If soils are chosen on similar slopes, exposures, and parent materials, they represent a precipitation-temperature sequence. It may not be possible to isolate the crucial individual moisture and temperature sequences (Figure 9).

In Iowa and Missouri the loess sheets vary systematically in composition from the river channels to the interior uplands. The soils change accordingly. The Iowa workers consider the age of the soil to vary in a parallel fashion, hence they speak of chrono-litho-sequences of soils (Hutton 1950).

While polysequences are helpful for purposes of system arrangement and soil sequence classification, they do not match the scientific value of the monosequences.

Continuities and Discontinuities

Factorial analysis sheds light on the current controversy on continuity and discontinuity of soils and vegetation. It appears profitable to distinguish two separate aspects of the problem; first, mapping procedures in the field, and, second, conceptual considerations as they arise in schemes of classification.

Soil survey activity and vegetation mapping operate with the discontinuity idea. On soil maps all soils are separated by boundaries. The soils are shown as discrete entities. The same holds true for plant associtions on vegetation maps, as illustrated by the impressive cartography executed by the Tüxen school. While transitions between types are sometimes conceded, in practice they are not recorded.

From the standpoint of state factor analysis the continuity concept of soils and vegetation is deserving of more explicit recognition in field work. The five principal functions offer the following criteria:

(1) If, in a given area, the five state factors vary continuously, soil and vegetation very likely will vary continuously also. Larger systems would be expected to diffuse into each other.

(2) If, in a given area, one or more state factors vary in a discontinuous fashion, soil and vegetation very likely will also exhibit discontinuities. In the field there will be lines of demarcation.

Among the five factors, parent material and topography are most commonly observed to change abruptly. Yet, even with these two, abruptness often is a relative thing. What may strike us as a sharp boundary in the field may not convey the same impression to a centipede. In fact, the recognition of gradual or sudden changes depends on the scale of mapping. The scale is seldom chosen on a scientific basis; more often the choice is governed by utilitarian motives, such as agricultural significance, cost of survey, personal convenience, in brief, practical expediency. There is, of course, nothing wrong with this attitude provided it is recognized as arbitrary.

On the conceptual level, such as system classification, continuity looms paramount, certainly in the realm of soils. Theoretically, one can pass from any soil type to any other by a series of infinitely small steps having equal classificatory significance. In ecology the situation is more controversial. Members of the Braun-Blanquet school of plant sociology, e.g. Tüxen, attribute to plant associations features of a type resembling an organism. Transitions, if at all recognized, are said to occur only as stepwise intervals; indeed, in the floristic definition of an association, a species is either present or absent. But in terms of vegetative growth or relative frequencies of species, continuity appears possible, as Curtis (1955) and Whittaker (1956) assert. Since soils can vary continuously, it follows—*sine qua non*—that vegetation and the larger system must be able to vary continuously also.

Summary

As a frame of reference for ordering the multitude of soils, pedology often makes use of the

pedogenic functions. In these the plant kingdom plays the role of both dependent and independent variable. It also appears as a "constant."

This paper attempts to circumscribe the plant biotic factor in soil formation and ecosystem development. Emphasis is placed on conceptual questions. They are answered by devising models and imaginary experiments that permit analysis of the five state factor functions, namely, bio-, litho-, topo-, climo-, and chronofunctions.

It is believed that these considerations possess interest for ecology as well as pedology.

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A DISJUNCT STAND OF HEMLOCK IN THE GEORGIA PIEDMONT

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During the spring of 1955 while making a floristic survey of the future site of Lake Ranier, Dr. W. H. Duncan discovered the first station for hemlock, *Tsuga canadensis*, in Hall County, Georgia. The station, located on a biotite schist or gneiss of precambrian origin at an elevation of approximately 1,000 feet, is on the east bank of the Chattahoochee River 3.4 miles below its confluence with the Chestatee River and 0.5 miles below Browns Bridge (Fig. 1). The hemlocks occurred in two groups about 125 meters apart on steep northfacing slopes rising from the water's edge. In this position they were on the outside of a long and gradually curving but at points undercutting meander, and faced across the broad flat valley of the Chattahoochee floodplain. These hemlocks represented the southernmost known outlier of hemlock in the state of Georgia being approximately 20 miles south of the hemlock stations in Lumpkin County.

Objectives of this study were (1) to ascertain the composition of the hemlock forest and the associated environmental conditions as a record for any future phytogeographical or ecological studies, and (2) to evaluate, within the limits of the collected data, the factors responsible for the success of hemlock in this location, and to attempt to determine whether it was contracting, expand-

FIG. 1. Composite photograph of a portion of the hemlock forest. See Figure 2 for exact location.

ing, or maintaining its range. Unfortunately, this botanically important vegetation was destined to be submerged by the newly developed Lake Ranier early in 1956. To approach these objectives within the time available and within the confines of regular academic duties a preliminary visit was made to the site in 1955. Crews of six and seven people then were mustered for two additional "task force" visits made during February of 1956. The gates of Buford Dam were closed early in February and within two months the area was completely submerged.

The authors are indebted to the following persons for their generous aid in analyzing the flora and soils of this habitat: flora, Dr. Wilbur Duncan of the University of Georgia and Mr. Haskel Venard of Atlanta, Georgia; mosses and liverworts, Dr. Lewis Anderson and Dr. Hugo Blomquist of Duke University; soils, Dr. Joel Giddens of the University of Georgia, Dr. William Ralston of Duke University, and Dr. A. B. Prince of the University of New Hampshire.

METHODS AND RESULTS

The occurrence of hemlock appeared to be correlated with slope and aspect. One of the first objectives was to determine this relationship, more precisely, through the construction of a topograpic map of the area. Using an Abney level, a forester's compass, and a topographic chain, a map with ten foot contour intervals was constructed (Fig. 2).

Vegetation was studied by means of observational cruises in which the relative importance of various species was noted. After preliminary observations the area was delimited into three zones based on vegetational- topographic relationships (Fig. 3). Each zone was then studied and the vegetation described. Due to winter conditions, considerable difficulty was experienced in compiling species lists. Undoubtedly some woody species were missed in the tangled growth and a few others were impossible to identify; also most of the herbaceous plants had been killed back by winter frosts. The species lists, therefore, are incomplete. Nomenclature, except where authori-

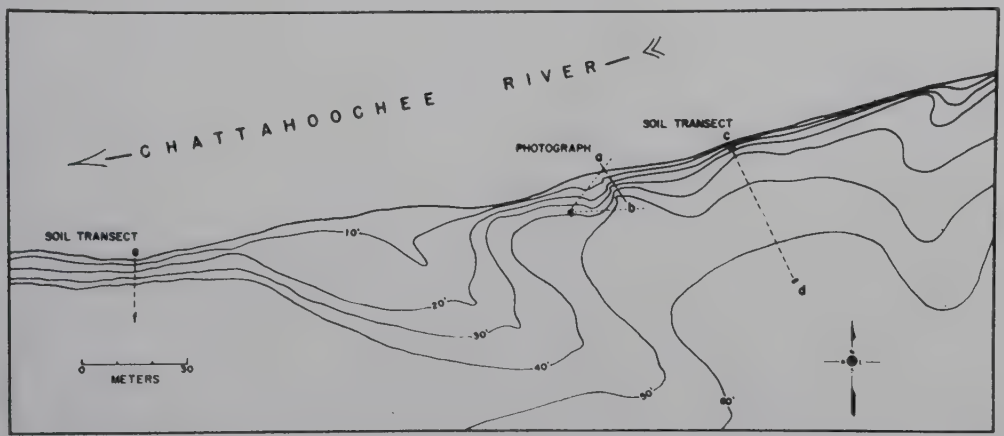

FIG. 2. Topographic map of the area showing the location of the photograph in Figure 1, the soil pits, and the soil transects.

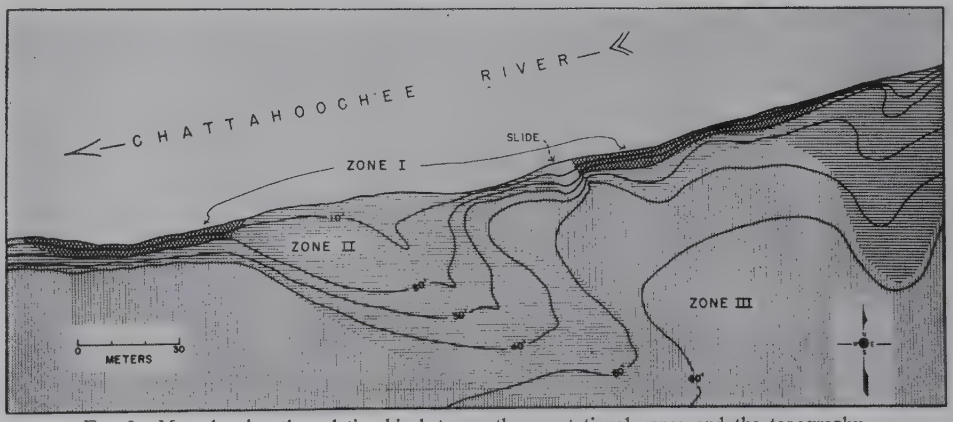

FIG. 3. Map showing the relationship between the vegetational zones and the topography.

ties are mentioned, follows Gray's Manual, eighth edition.

Zone I was a forested zone on steep, 36° to 51°, N and NNW facing slopes beside the river. This zone was characterized by the presence of large hemlock trees, an almost continuous overstory canopy, and a relatively open shrub layer. *Tsuga canadensis* formed the major component of the overstory canopy along with *Quercus alba.* Other trees of the canopy were *Q. rubra, Q. prinus, Liriodendron tulipifera, Fagus grandifolia, Acer rubrum, Betula lenta* (the first record for Hall County), and *Prunus serotina.* In one place a vigorous group of *Ilex opaca* trees 4 to 6 inches dbh formed a lower overstory. In addition to understory and transgressive trees, a number of shrubs were found within the forest. *Rhododendron maximum, R. punctatum* Andr., *Kalmia latifolia,* and *Leucothoe editorium* were common but formed a relatively discontinuous shrub layer. *Galax aphylla* and *Polystichum acrostichoides* were common herbs in this zone.

Zone II was found on the less precipitous slopes of ravines opening on the Chattahoochee and as a narrow band lying above steep Zone I slopes. This zone was characterized by an almost continuous cover of dense shrubbery over which spread an overstory canopy composed of much taller trees. Zone II differed from Zone I in the absence of *Betula lenta* and *Tsuga canadensis* (except for one sapling and a few seedlings) and in the thickness and continuity of its shrub layer. Major species of the shrub layer were *Rhododendron maximum,* confined to the bottoms and lower slopes of the ravines, *R. punctatum,* occurring throughout the zone, and *Kalmia latifolia,* occurring throughout Zone II and in part of Zone III. Additional shrub species were *Leucothoe editorum, Aesculus georgiana* Sarg., *Lindera benzoin, Aralia spinosa, Rhododendron* sp. The overstory was composed of *Quercus alba, Q. rubra, Q. velutina, Q. prinus, Fagus grandifolia, Acer rubrum, Liriodendron tulipifera,* and *Prunus serotina* with an occasional *P. echinata. Galax aphylla, Polystichum acrostichoides,* and *Epigaea repens* were found in the herb layer.

Zone III, on the gently sloping to flat sites above the slopes, was characterized by typical upland successional vegetation. About ten years ago this zone was dominated by a stand of 35 to 40 year old pine (probably *Pinus echinata*). At that time, however, most of the pine was cut and today a young open forest of *Pinus echinata, Quercus alba, Q. rubra, Q. falcata, Q. stellata, Acer rubrum, Cornus florida, Liquidambar styraciflua, Nyssa sylvatica,* and *Carya tomentosa* was found in the area. A very discontinuous shrub layer of *Kalmia latifolia, Rhus glabra, Viburnum* sp., *Vaccinium arboreum, Ceanothus americanus* and *Vitis* sp. was also found. *Andropogon virginicus, Erianthus contortus, Coreopis major,* and *Arundinaria tecta* were prominent herbs. This vegetation approximated that frequently encountered on cut-over disturbed uplands in this area.

The bryophyte flora was sampled by running three line transects through Zones I and II, and collecting all bryophytes occurring within one foot of either side of the line. Two of the transects paralleled those made for soils through the hemlock areas, and the third was made along the ravine at the eastern side of the experimental area. Collections have been grouped according to their zonal distribution, and the number of times each species occurred within the transects is indicated. Results are presented in Table I. Nomenclature follows that of vol. 43 of THE BRYOLOGIST.

TABLE I. Bryophytes collected from Zones I and II. (Number of times each species occurred in transects)

Liverworts	Zone I	Zone II
Calypogeia trichomanes	2	3
Diplophyllum apiculatum	0	3
Frullania asagrayana	3	2
Frullania Brittoniae	1	0
Frullania eboracencis	1	2
Frullania Kunzei	0	1
Frullania squarrosa	0	1
Leucolejeunea clypeata	7	5
Leucolejeunea unciloba	0	1
Microlepidozia setacea	2	0
Plectocolea crenulata	2	0
Plectocolea hyalina	3	0
Radula complanata	1	2
Radula obconica	1	1
Scapania nemorosa	2	0
Mosses		
Anomodon attenuatus	1	1
Anomodon rostratus	1	1
Atrichum angustatum	2	2
Aulacomnium heterostichum	2	1
Bartramia pomiformis	2	0
Campylium chrysophyllum	4	1
Cirriphyllum Boscii	4	0
Clasmatodon parvulus	2	3
Cryphaea glomerata	3	2
Dicranum scoparium	0	3
Diphyscium foliosum	4	3
Diplophyllum apiculatum	6	1
Drummondia prorepens	1	0
Entodon seductrix	0	1
Eurhynchium serrulatum	3	3
Homalotheciella subcapillata	1	0
Hypnum curvifolium	1	0
Leskea gracilescens	1	1
Leucobryum albidum	1	3
Leucodon julaceus	1	5
Orthotrichum ohioense	1	4
Platygryrium repens	0	2
Pogonatum pensilvanicum	0	1
Sematophyllum adnatum	1	5
Thuidium delicatulum	0	2
Tortella humilis	0	3
Ulota crispa	0	1

Counts, age, and dbh measurements were obtained on the hemlock trees growing in Zone I on both upstream and downstream slopes. Age estimates were based on successful increment borings made on nine trees. In the borings of downstream hemlock, a complete increment core was obtained from only one tree. All of the other trees had rotten centers. However, the age of one was extrapolated from a partial core. The ages of five seedlings were determined by cutting the lower stem, and counting the rings with a binocular dissecting scope. Counts of the number of larger trees in various diameter classes were made as were estimates of the numbers of seedlings in three seedling classes based on height. These data are presented in Table II.

TABLE II. Estimated numbers and age of hemlocks in various size classes on both slopes

Size Class	Slope 1 (Upstream)		Slope 2 (Downstream)	
	Estimated Numbers	Estimated Range of Age in Years	Estimated Numbers	Estimated Range of Age in Years
Height in Inches	Seedlings < 1″ dbh			
0 - 12	Few	4 - 9	100	4 - 9
12 - 24	0	-	10	7 - 8
24 - 36	0	-	1	?
Dbh in Inches	Trees > 1″ dbh			
1 - 3	0	-	0	-
3 - 8	7	57 - 59	0	-
8 - 14	5	63 - 72	3*	100
14 - 21	0	-	2	?
21 - 29	0	-	2†	135

*2 dead trees †1 dead tree

The age data indicates that hemlock in Zone I was not represented in continuous age classes. Rather it occurred in three age-range groups: 4 to 9, 57 to 72, and 100 to 135 years. A group of seven trees on the downstream slope was larger and older than the other groups. With the exception of one sound tree, this group appeared to be overmature. Three trees, whose crowns had broken off, were represented by stumps while three others had rotten centers. The group, with a dbh range of 10 to 27 inches, had an age range of 100 to 135 years. However, the higher age estimate may be subject to considerable error. The second group of hemlocks growing on the upstream slope approximately 125 meters from the first was smaller, 3″ to 14″ dbh, and younger, 57 to 72 years, than the first group. An eleven inch tulip poplar an a four inch black birch growing among the hemlocks were within the age range of that group, perhaps indicating that most of the tree vegetation originated at about the same time on that slope. The third obvious age group was one of seedlings less than three feet tall and 4 to 9 years old. This group was concentrated on the downstream slope in the upstream part of Zone I and in adjacent parts of Zone II.

Soils

Soils were studied in the field and in the laboratory. Two trenches were dug, one in Zone I (position c, Fig. 2) and the other in Zone III (position d, Fig. 2). The soil profile in each trench was described and sketched (Fig. 4) and a micromonolith of each profile was made. A volume weight sample was removed from each major horizon as was an additional sample for laboratory analyses. In the laboratory, samples were analyzed for major physical and chemical characteristics including texture, moisture equivalent, xylene equivalent, wilting percentage, pH, organic matter, and available phosphorous, potassium, and calcium. In addition to the trenches, soil transects were run on both the up and downstream slopes from Zone I to Zone III. The transects, shown in Figure 2 (c to d and e to f), were made by boring three foot auger holes at appropriate distances and recording the profiles.

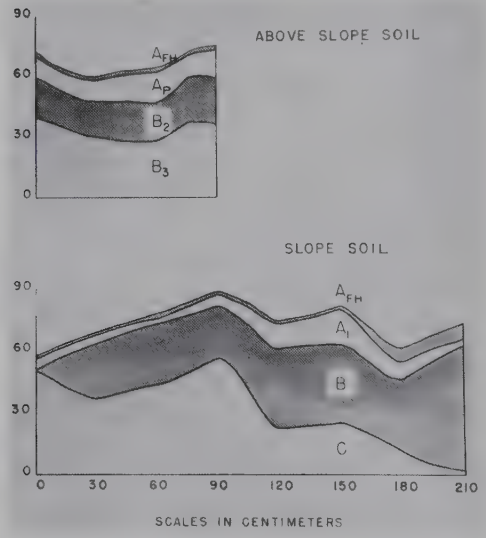

Fig. 4. Soil profiles from Zone III, above, and Zone I, below.

The trench in Zone I revealed a heavy concentration of roots in the upper six inches. This, plus the A_0 layer, probably held the soil against erosion, of which there were relatively few signs. The depth of the horizons was very variable (Fig. 4). The soil surface was covered with a 2-7 cm layer of oak, hemlock, and beech litter, underlain by a 1-4 cm fermentation layer. Beneath this was a black mull type humus layer from a trace to 5 cm thick. The mull graded imperceptably into a dark yellow brown sandy clay loam A_1 horizon 2½-17 cm thick. This horizon was characterized by a crumb structure and was extremely porous. Despite recent rains it was relatively dry. Under the A_1 was a granular, brownish-red sandy clay loam B_2 horizon that ranged from 0-60 cm in depth. This horizon, like the preceding one, was very porous and in places where the two horizons were thick it was possible to push an auger into the soil with very little effort. The B_2 horizon was moist and had many large roots. In some places they were concentrated at the transition between the B_2 and C horizons. No stones were present, but particles of mica, feldspar, and quartz were found. The C horizon was composed of sub-angular blocky, mottled red and yellow clay loam. Some lateral seepage was evident in this horizon in the walls of the trench. Few roots were present.

The trench in Zone III revealed somewhat less variable horizons (Fig. 4). The litter layer, composed of 2-5 cm of oak-pine litter, was underlain by a thin A_{fh} horizon. Beneath this was a 10-20 cm A_p horizon of gray brown sandy clay loam with granular structure and an abundance of roots. This horizon graded into a B_2 layer, 15-20 cm deep, composed of red yellow brown clay loam with sub-angular blocky to granular structure. Under this was a B_3 layer, 40-50 cm thick, composed of red pink clay loam with sub-angular blocky structure. Quartz, feldspar, and muscovite were present in both the B_2 and B_3 as were some roots. The C horizon of degraded rock was found at the bottom of the trench.

A comparison of profiles from Zone I and Zone III (Tables III and IV) indicates that the principal differences between the two are that the surface layers of the Zone I soil are exceptionally porous and of low bulk density. With the exception of a slightly larger amount of available K_2O in the B horizon of the Zone III soil, there seems to be no significant differences between zones in available CaO and P_2O_5, organic matter, or pH. Moisture equivalent, wilting percentage (with the exception of Zone I, A horizon), available water, xylene equivalent, and imbibitional water are also of the same magnitude in both profiles.

A possible difference between Zone I and III soils that did not appear in the soil analyses may be that water moving downslope over the subsurface rock layers was forced closer to the surface in the steep Zone I slope soils. This will be discussed later.

The data from the soil transect indicated that the soils in Zone I and III, with the exception of variations in the depth of horizons, were similar to the respective profiles exposed in the pits. The borings along the transect in Zone II indicated

TABLE III. Physical characteristics of soils

Horizon	Mechanical Analyses			Moisture Equivalent	Wilting Percent	Available H_2O	Xylene Equivalent	Imbibitional Water Value	Bulk Density	% Pore Space
	% Sand	% Silt	% Clay							
Zone I Soil (Slope)										
A_1	51	20	29	21.2	10.7	10.5	16.7	4.4	0.65	75
B	46	20	34	24.3	12.9	11.4	18.1	6.2	1.14	57
C	36	30	34	25.6	13.0	12.6	19.8	5.8	1.48	44
Zone III Soil (Above Slope)										
A	58	20	22	18.6	4.4	14.2	14.9	3.7	1.38	48
B_2	43	24	33	20.9	9.6	11.3	15.9	4.9	1.50	44
B_3	45	21	34	23.5	11.9	11.6	18.1	5.4	1.65	38

TABLE IV. Chemical characteristics of soils

Horizon	pH	Percent Organic Matter	Available Nutrients Lbs/Acre		
			P_2O_5	K_2O	CaO
Zone I Soil (Slope)					
A_1	5.0	3.2	8	140	300
B	4.7	1.1	2	96	200
C	5.1	0.2	6	52	200
Zone III Soil (Above Slope)					
A	4.5	3.0	8	136	200
B_2	5.2	1.0	5	156	200
B_3	5.2	0.6	8	220	300

that the underlying soil appeared to have characteristics intermediate between Zone I and Zone III soils. The soil transect, e-f, indicated essentially the same relationships as the c-d transect.

DISCUSSION

The hemlock forest, now submerged by the newly formed Lake Ranier, provided the first record of the species in Hall County and occupied the southernmost station for the species in the state of Georgia. This hemlock, growing on steep N and NNW facing slopes rising from the Chattahoochee River, was approximately 20 miles south of the nearest hemlock in the Chattahoochee-Chestatee River watersheds.

Similar disjunct hemlock stands occur in both North Carolina (Oosting and Hess 1956) and Alabama (Segars et. al. 1951 and Harper 1952). This stand and the North Carolina stand are found within the upper and lower Piedmont Province, respectively, while the Alabama stands occur in an extension of the Cumberland Plateau (Braun 1950).

The composition of the overstory, dominated by hemlock and white oak (*Quercus alba*), indicated that the slope vegetation bore some relationship to Braun's hemlock-white oak segregate of the mixed mesophytic forest association, while the abundance of *Rhododendron maximum* and *Kalmia latifolia* is perhaps indicative of relationship to the oak-chestnut association (Braun 1950). Although relationships of this slope forest are not entirely clear, it is certain that the forest was strikingly different from surrounding upland oak-hickory forests.

During visits to the site many hemlock trees with abundant crops of cones were noted. This, plus the presence of numerous seedlings, indicated that the trees produced viable seed.

Soil and water

Friesner and Potzger (1932) pointed out that the nature of the seed bed is of prime importance in the successful germination of hemlock. Its seedlings require a relatively open seed bed such as mineral soil or moss since they cannot penetrate a dense litter layer. Two phenomena natural to these slopes might be conducive to the development of favorable seedbed conditions for hemlock. Firstly, occasional floods such as the one on January 8, 1946, which crested twenty-six feet above normal (Paulsen 1952), inundated the slope. Water action of this kind cannot only remove litter but may also deposit materials. In fact most of the present group of seedlings probably started on a thin layer of flood deposited sand. Secondly, the river was undercutting the bank and occasionally pieces slid into the river

exposing bare slopes as is noted in Figures 1 and 3. Hemlock might have found suitable seedbed conditions during the course of revegetation of such slides. The youth and relatively even age of the upstream Zone I forest (Fig. 1) could be related to its initiation on a slide.

Mineral soil seedbeds alone are not sufficient in this region to assure hemlock germination and establishment. Approximately fifty years ago and for several years afterward mineral soil seedbeds, typical of abandoned fields, were probably available in Zone III close to hemlock seed sources in Zone I. Yet Zone III was invaded by pine, as shown by pine stumps, while there was no evidence of a hemlock tree that became established at the time of abandonment. Within the open forest left behind following the removal of pine many thinly littered or moss-lichen areas were available close to hemlock seed trees, but no hemlock seedlings were found there. Apparently there were other factors favorable to hemlock on the slope and unfavorable in Zone III.

Oosting and Hess (1956) working with a disjunct hemlock stand growing under similar north facing slope conditions discovered that insolation, temperature, and evaporation within the seedling stratum were lower on the slope than on the more level land immediately above the slope. The same set of conditions probably existed on Zone I slopes and contributed to the successful establishment of seedlings and to the conservation of soil moisture.

Analysis of soils in Zone I and III revealed no striking differences except in the low bulk density and high porosity of the soil under hemlock. The latter characteristics, also noted under hemlock by Daubenmire (1931), Oosting and Hess (1956), and Oosting and Bourdeau (1955), are probably the result of rather than the cause of hemlock.

One important difference between Zone I and Zone III soils that did not appear in the soil analyses and which may have been important in the success of older hemlock seedlings and trees on the slope was downslope lateral movement of water within the C horizon of the Zone I soils. Certain observations indicated the possibility that water moving downslope over rock layers may have been forced closer to the surface in the steep Zone I slope soils. The appearance of seepage water in the trench was evidence of seepage at least at the time the trench was dug. The mottled color of the C horizon which was absent in Zone III may have been due to long periods of poor aeration resulting from seepage water in the horizon much of the time. The general lack of roots in the C horizon may be further evidence of poor aeration within the zone, while the clusters of roots at the bottom of the porous B_2 and on top of the C horizon may have developed in response to availability of water in the latter horizon.

Coile (1952) suggested that water distribution on slopes in mountainous terrain is influenced to a large degree by sub-surface lateral seepage along relatively impermeable layers. On the basis of the above evidence this would seem to be the case under the Zone I slope forest. However, it would not be true for all slopes because lateral seepage is related to a number of factors. Among the more important are permeability, dip, and strike of the rock layers, depth of overlying soil layers, extent of the catch basin above the slope, the over-all topography as it influences sub-surface flow, and the amount of rain falling on the area. Considerations such as these might account for the differences between Potzger and Friesner's (1936) study area in Indiana where slopes, including northfacing ones, were drier than surrounding uplands and Oosting and Hess's (1956) study area in North Carolina where northfacing slopes were moister than surrounding uplands.

It should be stressed, however, that conditions on any slope are the result of a complex of factors of which sub-surface seepage is only one. Similar amounts of sub-surface seepage on north and southfacing slopes would probably be modified by the contrasting energy regimes of the two slopes so that the slopes would support different vegetational systems.

Reproduction

The occurrence of hemlock in three discontinuous age groups, 4 to 9, 57 to 72, and 100 to 135 years, on three different sites within Zone I indicated that the species was not steadily reproducing itself.

Successful reproduction seemed to have occurred in spurts. This agrees with Graham's (1941) findings in Michigan where during some periods, probably a sequence of dry years, no hemlock becomes established; at other times occasional trees in especially favorable spots may gain a foothold, whereas at still other times, when a series of moist years occurs, mass reproduction takes place.

Here it seems as though the fortuitous combination of circumstances necessary for successful establishment (seed supply, mineral seedbeds, and favorable weather conditions) occurred only within certain spans of years with relatively long unfavorable periods between. The first years would seem to be most critical since each year of age should tend to increase chances of survival (Friesner and Potzger 1944) and if sub-surface seepage is important, older seedlings could begin to utilize this source of moisture. Needless to say,

this uncertain method of establishment represents a hazardous situation for the maintenance of the species at this site.

History of the Stand

The question of whether this stand was a relict of Pleistocene vegetation as suggested by Oosting and Hess (1956) for their North Carolina stand or an advancing outlier of the main body of hemlock to the north is difficult to answer. This stand was not so far removed from other hemlock stands upstream that it is inconceivable that one or a few trees may have originated in the not too distant past from seed washed down the river and that the present stand owes its lineage to these original invaders. The precarious way in which hemlock was reproducing at this site seems to suggest this.

However, if the latter is true this does not necessarily imply that hemlock is generally expanding its range. For when a species range is changing it would seem that change would not always occur as a steady movement in one direction but often as an oscillatory process of extension and contraction with a net gain in one direction or the other.

This concept is well substantiated by the variations which have occurred in post-Pleistocene climates, and especially of those variations occurring within the Christian era. Although specific data is not available for the southeastern states, Brooks (1951) in reviewing the world literature notes that for the regions studied there is ample evidence of alternating wetter and dryer periods of one hundred years or less, as well as long term trends of hundreds of years time. Thus, the stand under consideration might have represented either a temporary oscillation or a brief period of expansion in the general trend of contraction.

SUMMARY

A recently discovered disjunct stand of hemlock in the Piedmont of Georgia was investigated and data on its floristic, pedologic, and topographic relationships are recorded. The persistence or invasion of hemlock here seems to have been favored by subsurface seepage and very steep north-facing slope which minimized the heating and drying effects of solar insolation.

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VARIATION IN THE PINE-INHABITING VEGETATION OF NORTH CAROLINA

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The great variations in the bark-inhabiting vegetation of lichens and bryophytes in eastern North America are evident to any botanist who has traveled in the region. Yet no studies of the broad relationships of the corticolous vegetation here have previously been made. This study aims to determine something of the nature of those variations in North Carolina, a state sharply divided into three distinct physiographic regions.

Recent studies of corticolous vegetation in Wisconsin (Culberson 1955a, Hale 1955) demonstrate vividly the importance of the substrate in

determining the composition of bark vegetation within floristically homogeneous areas. In northern Wisconsin, the cryptogamic vegetation on pine is strikingly different from that on the hardwoods. In North Carolina, *Pinus* is the most abundantly represented genus of trees. In the present exploratory study, limited to the vegetation on pine, the complicating influence of substrate specificity is reduced.

Thanks are due to the Duke University Council on Research for meeting the expenses of this study.

Methods

The line transect was selected as the basis for sampling. The transect and the sampling stations along it were determined by drawing a line from the eastern coast (Pamlico County) to the western edge (Cherokee County) of the state on a highway map. Parallel lines, drawn on either side of the first line at a distance representing 5 miles, delimit a transect band 435 miles long and 10 miles wide. Eighty-eight equidistant points, marked at intervals equivalent to 5 miles, segment the band and locate potential sampling stations.

The pine woodland found closest to the limit of segments and closest to the center of the band was selected for sampling. Although most stations are quite near the center, in some areas of intense agriculture or of dense population suitable stands remain only towards the edges of the band. Figure 1-A maps the 88 sampling points.

The 5 pines closest to the place where the automobile was stopped were selected for sampling, trees in the very margin of the woods and plants with a d.b.h. less than 10.2 cm. (4 in.) being excluded. A "cylindrical" quadrat 35 cm. high was used for the vegetation at breast height (1.4 m.). The 440 quadrats thus vary in size. The validity of data from such quadrats will be discussed. All lichens and bryophytes within the quadrat were collected for later identification and the d.b.h. of the tree was recorded.

The taxonomic determinations were complicated by the presence of much juvenile material. Immature plants, particularly in the *Parmelia perlata* complex, make up much of the vegetation and an accurate classification of such individuals has been attempted. Using Asahina's microchemical techniques for identifying lichen substances by the crystals produced in residues treated with crystallizing agents or with compounds reacting to form crystalline derivatives, it was possible to name most juvenile specimens. But the methods proved of value only for thalli wider than about 3 mm. Isidiate plants containing stictic acid are assigned to *P. crinita*, those with salacinic acid to *P. subcrinita*. Non-isidiate plants containing salacinic acid are called *P. reticulata* although this designation may include some *P. cetrata*. Non-isidiate plants containing stictic acid alone are called *P. trichotera;* those with both stictic and norstictic acids, *P. erecta* "A"; and those with norstictic acid alone, *P. erecta* "B." Of course they all contain atranorin.

The nomenclature of the lichens conforms to Hale and Culberson (1956), that of the mosses to Grout (1940) and that of the hepatics to Evans (1940). Dr. L. E. Anderson determined the mosses, Dr. H. L. Blomquist the hepatics.

Results

Figure 1-C shows the distribution, in comparison to geographic location (the stations in Fig. 1-A) and to elevation (Fig. 1-B), of tree species along the transect. The elevation data are from the North Carolina Geological and Economic Survey (1917) and the U. S. Coast and Geodetic Survey (1949). They represent the elevation at or very near the stations rather than a continuous profile along the center of the band. In Figure 1-C the data from the 88 stations are divided into 22 groups each including 4 successive stations and 20 trees. The data for *Pinus taeda* may include some for *P. serotina,* not distinguished in this study.

The Cryptogamic Vegetation

To evaluate the influence of variable quadrat size on results, the data for the commonest pine are analyzed. In Table I, the data from the 158 quadrats on *P. taeda* are classified into 5 groups by a measurement (d.b.h.) proportional to quadrat size. Both the mean and the modal number of species per quadrat are essentially the same for the quadrats of all size classes. The quadrats of the smallest size are then sufficiently large to include the same number of species found in the largest quadrats and the data are assumed to be comparable. Other studies of corticolous vegetations and of similar technique (Culberson 1955a, Hale 1955, Klement 1952) report like results.

Table I. The mean and the modal number of species per quadrat vs. the size classes of individuals sampled of *Pinus taeda* (*i.e.*, vs. quadrat size)

d.b.h. in in.	Number of trees	Number of Species	
		Mean	Mode
4- 6	10	3.2	3
7- 9	34	3.1	2
10-12	53	3.7	3
13-15	42	3.7	3
16+	19	2.9	2

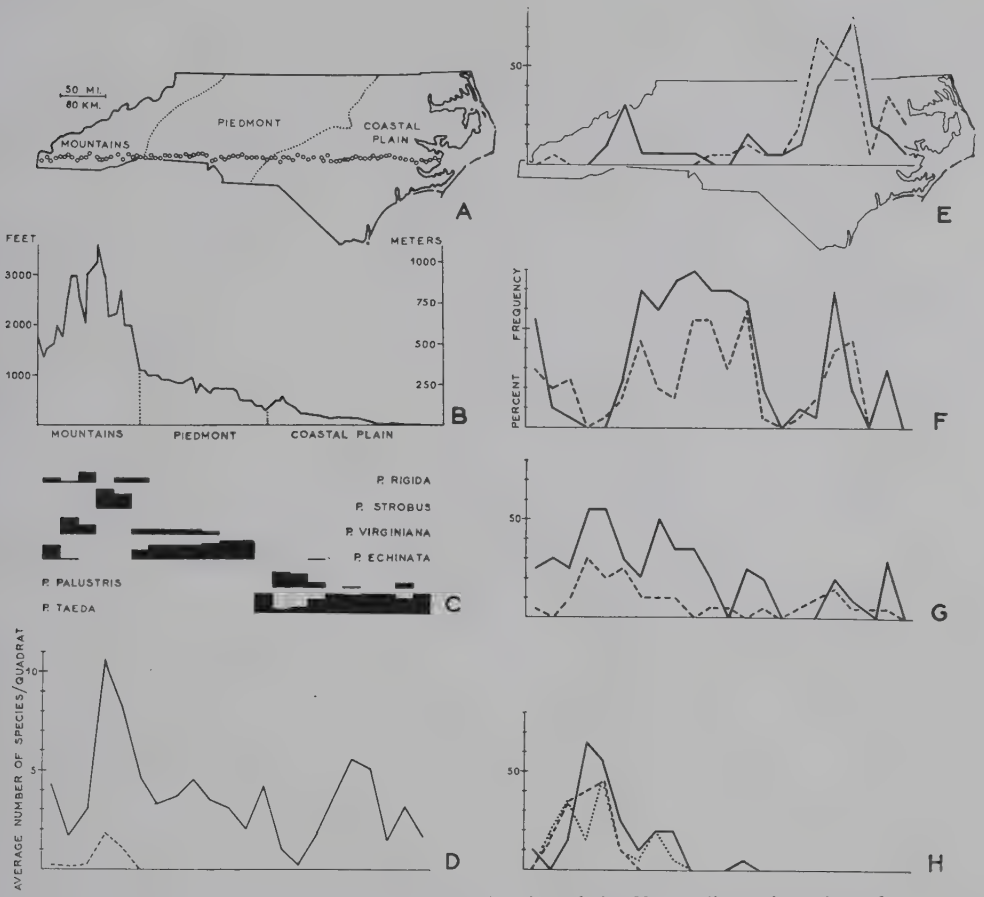

FIG. 1. A graphic summary of results. A. The location of the 88 sampling points along the transect. — B. The elevation of the sampling points. — C. The relative importance, as determined by frequency, of the species of pine along the transect. The height of the column indicates frequency within each of 22 intervals. — D. The average number of species of cryptogams (————) per quadrat and the portion of that average value contributed by bryophytes (- - - - -). The horizontal axis represents the transect divided into 22 intervals. — E-H. Species distribution based on frequency within 22 successive intervals. — E. Predominately coastal plain species. *Parmelia caroliniana* (————) and *Parmeliopsis ambigua*, usnic acid strain (- - - - -). — F. Broadly distributed species most common in the piedmont. *Buellia punctata* (————) and *Cetraria fendleri* (- - - - -). — G. Broadly distributed species more common at higher elevations. *Lecanora varia* (————) and *Parmelia rudecta* (- - - - -). — H. Mountain species. *Cetraria cilliaris* (. . . . .), *Parmelia caperata* (————), and *Usnea* spp., white medulla (- - - - -).

To determine the relative specific richness of the cryptogamic vegetation, the data from the 88 stations were again divided into 22 groups each containing 4 successive stations and 20 quadrats (20 trees). The average number of species per quadrat in each group is plotted at the midpoint of the appropriate interval along a horizontal axis corresponding to the transect itself (Fig. 1-D). The corticolous vegetation becomes richer in species from the ocean towards the upper coastal plain where it drops suddenly, to less than one species per quadrat, in the sandhills. The vegetation then becomes more diversified through the piedmont into the mountains. On pines at the highest elevations, the vegetation is luxuriant in form, complex in composition and the average number of species per quadrat may exceed 10 (23 species, nearly one-third the total number recorded in the whole study, occurred in each of two quadrats here). Bryophytes, in one quadrat in the coastal plain and in only a few in the upper piedmont, are important on pine only in the mountains. On the western slopes, the average number of species rapidly declines and approximates data

from the eastern piedmont. Although from a comparison of Figures 1-C and 1-D the relative species richness of the bark vegetation on the various species of pine may be surmised, Table II gives exact information.

TABLE II. The number of individuals (= the number of quadrats) sampled of the various species of *Pinus* and the average number of cryptogamic species per quadrat

Species	Number of Trees	Average Number of Species per Quadrat
P. palustris (longleaf pine)	41	0.3
P. rigida (pitch pine)	28	2.4
P. virginiana (Virginia pine)	49	3.2
P. taeda (loblolly pine)	158	3.4
P. echinata (shortleaf pine)	129	3.6
P. strobus (white pine)	35	10.0

In all, 76 species (66 lichens, 10 bryophytes) were found. The data from the 88 stations are divided into 11 groups, each with 8 stations and 40 quadrats, and the frequencies for the cryptogams in the several intervals are in Table III. Only the 40 most common species are listed, *i.e.* those with both an over-all frequency of 1.1 per cent or more (found in at least 5 of the 440 quadrats) and a constancy of 3.4 per cent or more (found in at least 3 of the 88 woodlands). The 36 rarest species are the lichens *Alectoria nidulifera* Norrl., *Anaptychia hypoleuca* (Mühl.) Vain., *Anzia colpodes* (Ach.) Stzb., *Bacidia chlorococca* (Graewe) Lett., *B. vernicoma* Tuck., *B.* sp., *Ce-*

TABLE III. The over-all frequency and constancy of the 40 most common cryptogams and their frequency in each of the 11 successive intervals (1 to 11 from west to east) into which the transect is divided. The location of each interval—in mountains, piedmont, or coastal plain—is indicated by M, P, or C respectively

Species of Cryptogams	Over-all Frequency	Constancy	M 1	M 2	MP 3	P 4	P 5	P 6	PC 7	C 8	C 9	C 10	C 11
Bacidia sp.	1.4	3.4	....	2	5	....	....	....	2	....	....	8	....
Buellia punctata (Hoffm.) Mass.	32.3	46.6	32	2	12	65	78	55	42	5	38	10	15
Buellia stillingiana Stein	3.4	6.8	....	15	22	....	....	....	....	....	....	....	....
Cetraria aurescens Tuck	1.6	5.7	....	8	10	....	....	....	....	....	....	....	....
Cetraria ciliaris Ach.	7.0	15.9	10	25	28	12	2	....	....	....	....	....	....
Cetraria fendleri (Nyl.) Tuck	22.5	45.4	25	12	12	32	35	42	35	2	28	22	....
Cetraria oakesiana Tuck	3.4	9.1	2	22	10	2	....	....	....	....	....	....	....
Cetraria tuckermanii Oakes	1.4	4.5	2	8	2	....	....	....	....	....	....	....	....
Cladonia coniocraea (Flk.) Sandst.	5.0	10.2	2	30	22	....	....	....	....	....	....	....	....
Cladonia delicata (Ehrh.) Flk.	34.8	61.4	32	8	22	15	28	22	25	28	78	60	68
Graphis scripta (L.) Ach.	1.1	4.5	....	10	2	....	....	....	....	....	....	....	....
Haematomma cismonicum Beltr.	1.6	3.4	....	15	2	....	....	....	....	....	....	....	....
Lecanora minutella Nyl.	14.8	33.0	15	15	18	32	22	15	12	....	15	5	12
Lecanora varia (Ehrh.) Ach.	22.0	46.6	28	40	42	35	35	10	22	....	10	5	15
Lecidea nylanderi (Anzi) Th. Fr.	1.8	4.5	....	10	10	....	....	....	....	....	....	....	....
Lepraria, yellow spp.	3.4	10.2	....	....	12	....	2	10	2	....	8	2	....
Lepraria, white spp.	61.6	79.5	62	68	62	80	98	88	58	18	65	28	52
Ochrolechia pallescens (L.) Mass.	1.4	3.4	....	12	2	....	....	....	....	....	....	....	....
Parmelia caperata (L.) Ach.	10.2	21.6	5	40	40	15	10	....	2	....	....	....	....
Parmelia carolinana Nyl.	13.9	30.7	....	....	20	5	5	....	10	8	48	48	10
Parmelia dissecta Nyl.	10.4	22.7	....	20	35	5	2	....	....	2	20	18	2
Parmelia erecta "A" Berry	2.5	6.8	....	....	....	....	....	....	....	....	10	18	....
Parmelia erecta "B" Berry	5.9	18.2	....	5	10	10	8	5	2	5	....	18	2
Parmelia pertusa (Schrank.) Schaer.	1.4	3.4	....	8	8	....	....	....	....	....	....	....	....
Parmelia reticulata Tayl.	6.1	14.8	....	18	12	2	8	....	....	....	5	8	2
Parmelia rudecta Ach.	8.2	27.3	2	20	22	10	5	5	2	2	12	5	2
Parmelia subquercifolia Hue	2.5	8.0	....	8	2	....	10	2	2	....	2	....	....
Parmelia trichotera Hue	1.8	5.7	....	....	....	....	....	....	....	....	8	8	....
Parmeliae Indeterminable	8.9	28.4	18	20	18	5	8	2	5	5	10	8	....
Parmeliopsis aleurites (Ach.) Lett.	5.4	15.9	8	10	15	2	15	....	2	....	8	....	....
Parmeliopsis ambigua (Wulf.) Nyl., usnic acid strain	13.0	28.4	2	....	....	....	....	5	8	12	60	28	28
Pertusaria multipuncta (Turn.) Nyl.	1.8	4.5	....	12	8	....	....	....	....	....	....	....	....
Usnea spp., white medulla	6.8	14.8	8	38	28	....	....	....	2	....	....	....	....
Usnea spp., red medulla	2.5	9.1	8	10	8	....	2	....	....	....	....	....	....
Unidentified crustose species A	1.1	4.5	....	....	....	....	....	2	....	2	8	....	....
Unidentified crustose species B	15.0	36.4	18	2	18	15	25	5	20	15	25	5	18
Bryophytes:													
Frullania asagrayana Mont.	3.4	6.8	....	30	8	....	....	....	....	....	....	....	....
Frullania eboracensis Gottsche	1.1	4.5	8	5	....	....	....	....	....	....	....	....	....
Leucolejeunia unciloba (Lindenb.) Evans	3.0	6.8	....	18	15	....	....	....	....	....	....	....	....
Microlejeunia ulicina (Tayl.) Evans	1.6	4.5	....	12	2	....	....	....	....	....	....	....	2

traria juniperina (L.) Ach., *Cladonia chlorophaea* (Flk.) Spreng. sen. lat., *C.* sp., *Dimerella diluta* (Pers.) Trev., *Lecanora pallida* (Schreb.) Rabh., *L. subfusca* (L.) Ach. sen. lat., *L.* sp., *Lecidea scalaris* Ach., *L.* sp., *Parmelia cladonia* (Tuck.) DR., *P. crinita* Ach., *P. formosana* Zahlbr., *P. physodes* (L.) Ach., *P. revoluta* Flk., *P. saxatilis* (L.) Ach., *P. subcrinita* Nyl., *P. sulcata* Tayl., *Parmeliopsis ambigua* (Wulf.) Nyl. [divaricatic acid strain = *P. hyperopta* (Ach.) Vain.], *P. placorodia* (Ach.) Nyl., *Pertusaria amara* (Ach.) Nyl., P. *pertusa* (L.) Tuck., *P.* sp., *Physcia tribacoides* Nyl., *Ramalina fastigiata* (Pers.) Ach. and the bryophytes *Dicranum montanum* Hedw., *Hypnum reptile* Mx., *Orthotrichum* sp., *Platygyrium repens* (Brid.) Bry. Eur., *Sematophyllum adnatum* (Mx.) E. G. Britton, and *Ulota* sp.

Since there is no previous information on the quantitative distribution of cryptogams in North Carolina, several species are selected to illustrate distributional patterns. In Figures 1-E-H each point represents the percentage frequency for a species within an interval of 4 stations along the transect. The frequencies graphed are for the 22 intervals as in Figures 1-C and 1-D rather than the less detailed data for the 11 intervals of Table III.

Discussion

In the distribution of number of species (Fig. 1-D), one is impressed by the great richness of the vegetation in the mountains and by the low number of species in the vegetation of the upper coastal plain, the sandhills area. Of course different species of pine are involved. In other words, the bark vegetation along the transect is not only subject to environmental differences associated with variations in elevation, but also to differences in substrate (the bark of different species).

The influence of the substrate is difficult to evaluate because the species of pine are not broadly mixed throughout North Carolina. That substrate differences contribute to variations in the composition of bark vegetations on pines as compared to those on hardwoods is well-known. In Wisconsin, significant differences, both in the average number of species per quadrat and in the species composition, were found in the cryptogamic vegetation on pines as well. That *Pinus strobus* and *P. rigida,* frequently growing close together if not actually associated in North Carolina, support greatly different average numbers of species per quadrat (Table II) may indicate that substrate factors are involved in determining the composition of bark vegetations in the mountains here. Nevertheless, again in Wisconsin, the average number of species on *Pinus banksiana* and on *P. strobus,* in disjunct stands in the southern half of the state, is much lower (by about 4 times) than the average number of species on the same pines in northern Wisconsin. There, in a region of modest relief, the increase in number of cryptogams on a single species of pine is correlated with latitude. It would seem then that the increase in species numbers towards the mountains in North Carolina might be explained largely by factors other than those of the substrate; namely, factors related to elevation, particularly humidity. That increased precipitation, lower temperatures, and a high precipitation-evaporation ratio favor a vegetation rich in species and in luxuriance of development is known from studies elsewhere, *e.g.,* in Scandinavia (Almborn 1948), in France (des Abbayes 1934), in Italy (Cengia Sambo 1928), and in Wisconsin (Culberson 1955b). The high similarity of the vegetation on pines in the mountains of North Carolina to that on pines in the northern conifer-hardwood forest of the Lake States and of New England is shown by the presence of such species as *Cetraria ciliaris, C. oakesiana, C. tuckermanii, Parmelia pertusa,* and the less frequent *Alectoria nidulifera, Parmelia cladonia, P. physodes, Dicranum montanum, Hypnum reptile,* and *Ulota* sp., all totally lacking or extremely rare in the piedmont.

The water relations may also account for the low average number of species per quadrat in the sandhills at the inland limit of the coastal plain. Here, where trees are widely spaced, where much of the soil surface is bare, exposing the white sand, "aerial aridity due to reflection of radiation" (Wells and Shunk 1931) is doubtless a powerful factor contributing to the dearth of corticolous cryptograms. Aside from the severe water relations, the preponderance of fire—the factor accounting in fact for the very maintenance of pinelands in the coastal plain—cannot be overlooked. In almost every pine stand in the coastal plain past fires are evidenced by charred trunks, blackened in many forests to a man's height. Ground fire is surely detrimental to corticolous cryptogams at breast height on pine, but it hardly explains the difference in the average number of species on *P. taeda* (3.4) and on *P. palustris* (0.3) since both pines are subjected to fire, at least periodically. Perhaps the "aerial aridity" of the sandhills is indeed responsible for the paucity of vegetation on *P. palustris,* a tree of which 85 per cent of the sampled individuals supported no cryptogams whatsoever.

The frequencies in Table III show that even the 40 most common cryptogams are of fairly precise geographic distribution and, needless to say, almost

all of the 36 rarest species, excluded from the table, are very restricted. In fact, extreme environmental sensitivity, shown in so many studies of cryptograms, makes a report of a broad amplitude of tolerance suspect of faulty taxonomy. In our study, however, some species reported across the state are unquestionably uniform in morphology. *Buellia punctata* and *Cetraria fendleri* (Fig. 1-F), wide-ranging species most common in the piedmont, are sufficiently unique to preclude question and *Parmelia caroliniana,* with its unusual coastal plain and mountain distribution (Fig. 1-E) is the subject of a recent taxonomic and chemical study (Culberson 1957). But certain other records of broad distributions are less certain. Those for the imperfect lichen *Lepraria,* for example, are essentially meaningless. They surely contain several morphologically indistinguishable entities and perhaps extremely juvenile forms in other genera. "Unidentified crustose species B," always sterile, shows a considerable variation in form. The records for *Cladonia delicata* also include some for the coastal plain species *C. ravenelii,* the sterile squamules of both being very similar.

In assessing the graphs (Figures 1-E-H) it is necessary to recall that the data pertain only to distributions on pine. For such predominately pine-inhabiting species as *Parmelia caroliniana, Parmeliopsis ambigua* (usnic acid strain), *Cetraria fendleri,* and *C. ciliaris,* the graphs of frequency very closely approximate the total distribution. On the other hand, *Parmelia rudecta* and *P. caperata,* which on pine tend to be more frequent at higher elevations, are actually widespread on hardwoods in the piedmont, and, to a lesser extent, on the coastal plain. Likewise bryophytes are abundant on hardwoods at lower elevations.

The distributional patterns now delimited for the cryptogams are similar to those known for the flowering plants.

Summary

1. The bark vegetation at breast height was sampled by quadrats on 5 pines at each of 88 points along a transect 435 miles long from the eastern coast of North Carolina to the western edge of the state. Frequencies were determined for the 76 species (66 lichens, 10 bryophytes).

2. The richness in species of the corticolous vegetation increases rapidly from the ocean across the coastal plain. In the sandhills, where atmospheric humidity is low and where fire is frequent as everywhere in the coastal pine forests, the average number of species per quadrat drops to less than one. Through the piedmont to the mountains the bark vegetation progressively increases in numbers of species. The average number of species may exceed 10 at the highest elevations where precipitation-evaporation conditions are probably optimum in the state. Bryophytes are of importance on pine only in the mountains.

3. Frequencies in successive intervals of the transect are given for the 40 commonest cryptogams and graphs are provided for several species to illustrate typical quantitative distributions. The distributions are similar to those known for higher plants.

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RELICTS OF CLIMAX VEGETATION ON TWO MESAS IN WESTERN NORTH DAKOTA

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Vegetation that never has been grazed by domestic livestock is exceedingly uncommon throughout the mid-continental grasslands. In the course of field work in range conservation the authors in 1955 discovered two ungrazed mesas in a remote section of the area known as the Little Missouri River Badlands in western North Dakota. Livestock may be given access to the largest of these two mesas in the near future. Attempts had previously been made to construct a stock trail to its top; these efforts were being renewed in 1956.

Qualitative data were recorded on the mesas in April of 1956. It was determined at that time that certain quantitative data should be obtained at the end of the growing season for an enduring record. This was done on September 18 and 19, 1956. No other quantitative records of undisturbed vegetation of the area have been published; the nearest are those by Wright and Wright (1948) from some 300 miles west, and those by Larsen and Whitman (1942) from about 300 miles south-southeast. The writers were accompanied on both visits to the mesas by Dr. E. J. Dyksterhuis, Range Conservationist, Northern Plains States, SCS, Lincoln, Nebraska, and Mr. J. W. Turelle, State Soil Conservationist, SCS, Bismarck, North Dakota. Their direction and assistance with the study is acknowledged and greatly appreciated. We also are indebted to Mr. A. Francis Bahr, Area Soil Scientist, SCS, Dickinson, North Dakota, for examining and describing the soils.

DESCRIPTION OF STUDY AREA

The tops of the two mesas are separated by about a mile of much lower terrain (Fig. 1). One has a surface of about 12 acres and the other of two acres in two segments connected by a narrow ridge. Being unnamed, the mesas were called "Big Top" and "Two-Top," respectively, and are so designated in this report. They are located in North Dakota some 30 miles east of the Montana state line and 70 miles north of South Dakota, specifically, in sections 9 and 10, T. 144, R. 101, Billings County, North Dakota.

The soil on both mesas was classified as a Morton silt loam, representative of virgin Chestnut soil profiles. On Big Top mesa an underlying clay loam layer was found at an average depth of about 3 feet. On Two-Top mesa this layer occurred at a depth of approximately 2½ feet. These soils are considered typical of the "silty range site" being mapped by several agencies in rangeland classification. The vertical distance from the tops to the broad valley floor was estimated to be about 400 feet.

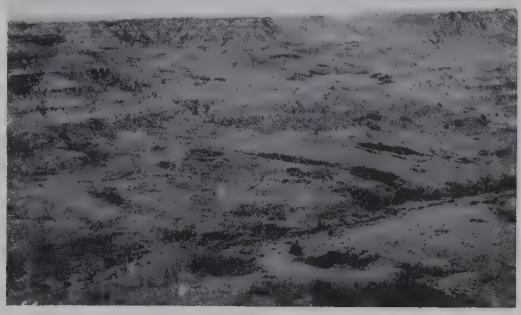

FIG. 1. Big Top mesa in the central background as seen from Two-Top mesa. Among the many mesas in the area, only these two are known to have never been grazed by domestic livestock.

Average annual precipitation is about 15 inches, with 12 inches received in the period April through September. Average dates of last killing frost in spring and first killing frost in fall are May 20 and September 15, respectively.

Mr. Ben Northrup, a rancher who has resided in the vicinity since 1933 supplied the information that hay had been cut once on Big Top mesa in the severe drought of the mid 1930's. Haying was accomplished by leading two horses to the top and hauling up a mower and rake with a rope and pulley. Then the hay crop was taken off by dropping it over the rim. He also verified our conclusion that neither mesa had ever been grazed by domestic livestock.

Tracks in dried mud and droppings indicated that one or a few deer might occasionally graze the top of Big Top mesa and that coyotes had hunted the tops of both mesas. Some digging had been done by badgers. Droppings indicated the presence of cottontail rabbits. Mice appeared to be quite numerous judging from their runways through the matted old grass. Snakes and cast skins of snakes were unusually common. One snake was captured and identified as a blue racer (*Coluber* sp.).

Scattered scrubby woody plants characterize portions of the precipitous mesa slopes wherever the skeletal soils or joints in the rock provide water and nutrients.

The mesas are characterized by a luxuriant unbroken cover of grass on flat relief with only an occasional shrub except near the rapidly eroding margins. Although there is little difference in soil and climate between top and floor, there is a great difference in the vegetation. Accessible areas in valley floors, as well as on nearby mesas easily reached by grazing animals, plainly reflect the effects that grazing has had in altering both the kind and amount of plant cover. Grazing by domestic livestock started in this area in about 1880.

Effects of drought and grazing upon the dominants of the climax were reported by Whitman, Hanson, and Peterson (1943).

Methods

Five methods were used in studying the vegetation. Ring counts in burn scars on junipers at the top edges of the mesas and ring counts on cross sections of the largest shrubs on the mesas were used to deduce fire history.

Circular plots one square meter in area were clipped at locations selected to be representative of the three types of plant communities that could be distinguished on the two mesas. Procedure in clipping, segregating, and naming materials followed that described by Dyksterhuis and Schmutz (1947). A mechanical arrangement of points in a gridiron pattern covering the top of each mesa was used to determine relative coverage by species of seed plants. The plant emerging from the ground at each point was identified and tallied. On Big Top, 400 such mechanically randomized points were recorded, and on Two-Top 240 points. Species too infrequent to be tallied in this sampling procedure were recorded separately with the intent of providing a complete list of species present. Two line-interception transects were read on Two-Top mesa using the procedure described by Canfield (1941). The locations were permanently marked with iron stakes so that the lines may be read again in later years, particularly in times of great drought when such readings can provide an indication of effects of drought on relative coverage by species, independent of grazing effects.

Results

Fire-scarred living trees could be found just over the rim of Big Top mesa and it was assumed that any fire there would also have burned over the mesa top. There was evidence, from ring counts, of a fire 16 or 17 years earlier. Ring counts of the larger big sagebrush (*Artemisia tridentata*) plants found on this mesa indicated an age of 16 and 17 years, thus verifying that a fire might have occurred about 1940.

There was no evidence of fire on Two-Top mesa or on its side slopes. One of the larger plants of big sagebrush appeared to be 47 years old. Large plants of big sagebrush that had been dead for several years also were found. One clump of Rocky Mountain juniper (*Juniperus scopulorum*) consisting of five stems with the tallest about 10 feet high on Two-Top mesa was the only tree growth that had become established on either mesa.

The results of the clipping studies to determine air-dry weight of herbage or forage, as well as of humic and fresh mulch corresponding to the Ao and Aoo horizons of soil science, are given in Table I.

Table I. Air-dry weight of forage, fresh mulch, and humic mulch from relicts of climax plant communities on normal silty loam soil under 15 inches of average annual precipitation in western North Dakota, September 1956

Plant community and location	Class of plant material	Pounds per acre
Stipa comata-Koeleria cristata Big Top Mesa	Forage	1,990
	Fresh mulch	2,920
	Humic mulch	2,400
	Total	7,310
Agropyron smithii Big Top Mesa	Forage	2,340
	Fresh mulch	5,130
	Humic mulch	8,600
	Total	16,070
Agropyron smithii Two-Top Mesa	Forage	2,070
	Fresh mulch	4,820
	Humic mulch	9,770
	Total	16,660
Agropyron dasystachyum Two-Top Mesa	Forage	3,110
	Fresh mulch	4,710
	Humic mulch	10,170
	Total	17,990

From Table I it may be noted that weight, expressed in pounds per acre, was remarkably similar on the two mesas if data from the same type of plant community are compared. Thus in the *Agropyron smithii* community, the weight of forage or herbage was a little over a ton per acre while fresh mulch weighed about two and one-half tons per acre and humic mulch weighed almost five tons per acre. A line-interception transect in this type of community indicated basal coverage by species as follows: *Bouteloua gracilis* 43%, *Agropyron smithii* 20%, *Stipa viridula* 17%, *Stipa comata* 11%, *Artemisia frigida* 6%, and *Agropy-*

ron dasystachyum 3%. Thus, type, as judged from aspect of total coverage, may bear little relation to measurements of basal coverage at the ground-line. In this case, the short blue grama was almost completely hidden by the taller wheatgrasses when viewed at an angle from a standing position. However, in certain portions of the *Agropyron smithii* type, this species undoubtedly ranges up to 100% of basal coverage.

The weight of humic mulch is probably least subject to fluctuations within the year and from year to year. Its amount in this case must reflect the approximate poundage to which it accumulates in reaching dynamic equilibrium between annual additions from growth of previous years and mineralization through decay. The five tons of humic mulch per acre here compares with two and one-half tons of humic mulch per acre measured by Dyksterhuis and Schmutz (1947) on relicts of climax grassland near Fort Worth, Texas. Our area receives less than half as much precipitation but the consequent lesser growth of vegetation is more than offset by the slower rate of decay associated with latitude 47° compared with latitude 33° at Fort Worth.

The weight data from the other two communities, as given in Table I, indicate that the *Stipa comata-Koeleria cristata* community produced almost as much herbage as the *Agropyron smithii* community but that old growth decayed much more rapidly. The *Agropyron dasystachyum* community was plainly the most productive with one and one-half tons of forage. The accumulation of fresh mulch and humic mulch combined is only slightly greater than in the other wheatgrass communities. A line-interception transect in this community indicated 100% basal coverage by *Agropyron dasystachyum* over a distance of 15 feet.

Relative coverage by species of seed plants as determined from a grid of 640 mechanically randomized points covering the main bodies of the mesa tops is shown in percentages as follows: *Agropyron smithii* 44.06, *Bouteloua gracilis* 20.94, *Agropyron dasystachyum* 13.59, *Koeleria cristata* 5.47, *Stipa comata* 5.16, *Carex filifolia* 2.34, *Stipa viridula* 2.19, *Carex eleocharis* 1.56, *Artemisia frigida* .94, *Lactuca pulchella* .78, *Poa canbyi* .63, *Calamagrostis montanensis* .31. Nine other species recorded once or twice but not always on both mesas totaled 2.03% and included the following: *Artemisia tridentata, A. cana, Opuntia polycantha, Helianthus rigidus, Sphaeralcea coccinea, Lygodesmia juncea, Solidago sp., Tragopogon pratensis,* and *Erigeron canadensis.*

From the foregoing it may be noted that six species of grasses and two sedges account for almost all of the vegetation. The two wheatgrasses (*Agropyron smithii* and *A. dasystachyum*) of mid-grass life form occupied over half of the total basal area while a short grass (*Bouteloua gracilis*) occupied a fifth. When viewed from above with a full year's growth present, the difference in stature would result in converting these measurements of 58 and 21 percent basal coverage, respectively, to estimates of total coverage approximating 70 percent for the two wheatgrasses and 10 percent for blue grama.

The two wheatgrasses are difficult to distinguish with certainty and on grazed ranges it is often impossible. They appear to have much in common ecologically as well as taxonomically. However, *Agropyron dasystachyum* was far more abundant on Two-Top mesa than on Big Top. This was associated with and may have been caused by the longer period without fire and the absence of a single mowing previously noted. Big sagebrush (*Artemisia tridentata*), too, was more abundant on Two-Top mesa. But even there it occupied so small a part of the surface that it was hit only twice in 240 mechanically randomized points. On Big Top mesa it was not hit in 400 points but *A. cana* was hit twice. Both species are far more abundant on the eroding slopes of the mesas and on the grazed valley floors.

A number of species were observed on the mesa tops but in such small numbers as to have been missed by the sampling reported previously. The record of species present in the climax should include the following: *Achillea lanulosa, Agropyron spicatum, A. trachycaulum, Allium sp., Andropogon scoparius, Artemisia gnaphalodes, Aster ericoides, Chrysothamnus graveolens, Circium undulatum, Linum lewisii, Monarda sp., Muhlenbergia cuspidata, Ratibida columnaris,* and *Vicia americana.* On spots recently disturbed by burrowing animals there were annual species of *Chenopodium, Euphorbia, Helianthus,* and *Salsola.* It is interesting that not a single specimen of an annual grass was found on either mesa. Also, *Buchloe dactyloides* (buffalograss) was absent.

Several species of plants were very common on the rapidly eroding margins of the mesas but rare or absent on the mesa tops. Among these were: *Artemisia tridentata, Atriplex confertifolia, Calamovilfa longifolia, Chrysothamnus graveolens, Eurotia lanata, Juniperus scopulorum, J. horizontalis,* and *Opuntia polycantha.*

Under protection from livestock grazing it was concluded that roughly two-thirds of the annual foliage production was yielded by western wheatgrass (*Agropyron smithi*) and thickspike wheat-

grass (*A. dasystachyum*). Species of *Stipa,* which also are cool-season mid-grasses, probably rank second in foliage production and *Bouteloua gracilis* third.

There were indications of the dynamic nature of climax plant communities. Thus, on Big Top mesa western wheatgrass was currently encroaching upon a community of *Stipa comata, Koeleria cristata,* and *Bouteloua gracilis.* This could be seen in lines of junction between the two communities which were distinct and abrupt. Plants of western wheatgrass along the advancing front produced more seed heads, longer rhizomes, and taller foliage (Fig. 2).

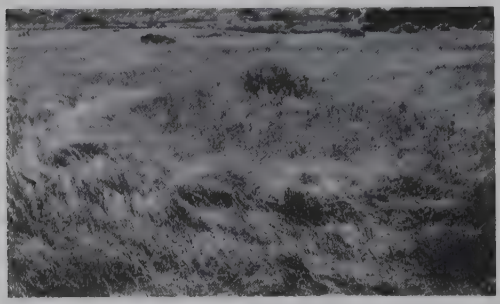

FIG.. 2. Close-up showing an almost pure stand of *Agropyron smithii* in the foreground. To the sides it is advancing into a community of *Stipa comata, Koeleria cristata,* and *Bouteloua gracilis,* marked in its center by a single plant of the shrub *Chrysothamnus graveolens.* Note that the line of advance is marked by a fringe of taller *A. smithii* reflecting less competition than where this wheatgrass is competing with a full stand of the same species. The advance is made with rhizomes rather than through establishment of seedlings. September 1956.

The soils underlying the two communities shown in Figure 2 apparently were the same, eliminating this as a factor which might govern the existing vegetative pattern. Slope of the land was slight and appeared to have little if any effect on this pattern. Since patterning was far more evident on the mesa where fire had occurred about 16 years before, it is possible that these phenomena are related. Although blue grama had considerable basal area on both mesas, even in areas of western wheatgrass dominance, the plants lacked vigor and often consisted of only two or three shoots. On Big Top mesa there were many dead crowns of this species which had not yet rotted away. It is important, however, to note that the short blue grama and dryland sedges will, nevertheless, survive in intimate mixture with the mid-grasses. Thus, they are present to begin increasing when conditions become less favorable for the mid-grasses. This is known to occur under close grazing or repeated close mowing.

It appears that big sagebrush, another common increaser under close grazing, occurs in climax vegetation of this site but its part of the total annual foliage production probably does not exceed 1 or 2 percent. The data from these two small mesa relicts are readily reconciled with results of numerous researches on grazed ranges of western North Dakota, reported by Drs. H. C. Hanson and W. C. Whitman.

SUMMARY AND CONCLUSIONS

Relicts of climax vegetation were discovered in 1955 on two mesas in western North Dakota. Data were taken in the spring and fall of 1956. The mesas, separated by a distance of a mile, are completely surrounded by precipitous slopes. They remain ungrazed by domestic livestock and virtually ungrazed by big game. The larger mesa was burned over about 1940 and the other apparently escaped fire for a half century or more. The site is characterized by 15 inches of average annual precipitation and normal Chestnut deep silt loam soil.

The plant cover, including surficial organic materials of all kinds, accumulates to the amazing total of eight tons per acre air-dry. Of this amount about one ton is herbage, two tons are fresh mulch in which leaf forms are clearly discernible, and five tons are humic mulch between the layer of fresh mulch and the mineral soil.

The climax is characterized by overwhelming dominance of *Agropyron smithii and A. dasystachyum.* Two other cool-season mid grasses, *Stipa comata* and *S. viridula,* are important, sharing a secondary position in the total cover with *Bouteloua gracilis,* and a short form of *Koeleria cristata.*

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THE EFFECT OF DRAINAGE ON THE ESTABLISHMENT AND GROWTH OF POND PINE (*PINUS SEROTINA*)[1]

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INTRODUCTION

In the fall of 1953 the writers had an opportunity to study the effects of good and poor drainage on the ecological development of contiguous stands of pond pine (*Pinus serotina* Michx. f.). These stands are located in the Waccamaw area of Brunswick County, North Carolina, 2.5 miles southeast of Exum, on Riegel Paper Corporation holdings. Thirty years prior to this study, both sites supported an impenetrable tangle of lianas and shrubs characteristic of the pocosins of the southeastern coastal plain. The area is known as Green Swamp.

The history of the present cover begins following a 1931 burn of the entire area. The ages of the pines indicate that they became established after the 1931 fire and before 1940. During the winter of 1939-1940 a logging road was built through the area in a generally east-west direction. At that time a dragline canal was constructed along the north side of the road. As a result of this construction, the area north of the road became a well-drained area, while that south of the road remained poorly-drained. It is the purpose of this paper to compare the woody vegetation which has subsequently developed on these two sites.

METHODS

A trail was cleared crossing the logging road at right angles and extending into the well-drained site to the north, and into the poorly-drained site to the south. As part of a separate study of water table fluctuation and drainage characteristics, a series of 8 drawwells was placed along this trail on each side of the road. On the well-drained side these were 33, 66, 99, 165, 231, 363, 495, and 759 feet, respectively, from the road, while on the poorly-drained side they were placed at 33, 66, 132, 198, 330, 462, 726, and 990 feet. For the vegetation analysis, base lines were laid out parallel to the road and extending 33 feet on either side of each drawwell.

A quadrat, 11 x 33 ft. in size (8.33 milacres), was placed on either side of each well, with the base line forming that side nearest the road. Within each large quadrat, a pair of 6.6 x 6.6 ft. (1 milacre) quadrats was placed randomly along the base line.

Six size categories were recognized. In the large quadrats on the well-drained site, overstory trees (those comprising the canopy) and understory trees (those over 12 feet tall, but not in the canopy) were counted and their diameters at breast height were recorded. On the poorly-drained site, because the trees were smaller and sparsely distributed, an overstory-understory stratification had not developed. Therefore, all plants over 12 feet tall were treated as overstory. In the smaller paired quadrats seedlings and shrubs were counted and placed in one of the following four basal diameter classes: Less than .25 in., .25 to .5 in., .5 to 1.5 in., and greater than 1.5 in. For purposes of this report, these four

TABLE I. Stem count, density (d), and frequency (f) of the woody plants less than 12 ft. tall on contiguous well-drained and poorly-drained sites. Thirty-two 1-milacre quadrats were counted on each site

Species	Well Drained Site			Poorly Drained Site		
	Total stems	d	f	Total stems	d	f
Acer rubrum L.	45	1.4	62.5	84	2.6	81.3
Chamaecyparis thyoides (L.) BSP.	39	1.2	46.9	10	0.3	21.9
Clethra alnifolia L.	271	8.5	68.9	121	3.8	50.0
Cyrilla racemiflora L.	37	1.2	43.8	690	21.6	96.9
Gaylussacia dumosa var. *Bigeloviana* Fern.	...	....	....	4	0.1	6.3
Gelsemium sempervirens (L.) Ait.	25	0.8	34.4	10	0.3	12.5
Ilex coriacea (Pursh) Chapm.	102	3.2	43.8	74	2.3	37.5
I. glabra (L.) Gray	...	...	....	53	1.7	31.3
I. myrtifolia Walt.	16	0.5	18.8			
I. vomitoria Ait.	6	0.2	12.5			
Lyonia lucida (Lam.) K. Koch	277	8.7	84.4	188	5.9	65.6
Magnolia virginiana L.	9	0.3	12.5	26	0.8	25.0
Myrica pensylvanica Loisel.	37	1.2	31.3	160	5.0	68.8
Nyssa sylvatica var. *biflora* (Walt.) Sarg.	13	0.4	18.8	78	2.4	78.1
Persea Borbonia (L.) Spreng.	61	1.9	62.5	73	2.3	56.3
Pinus serotina Michx. f.	...	...	....	5	0.2	12.5
Smilax Bona-nox L.	...	...	....	3	0.1	9.4
S. laurifolia L.	109	3.4	68.8	258	8.1	81.3
S. rotundifolia L.	99	3.1	81.3	9	0.3	12.5
Taxodium distichum (L.) Richard	...	...	....	3	0.1	9.4
Vaccinium spp.	10	0.3	15.6	10	0.3	12.5
Viburnum nudum L.	...	...	....	10	0.3	6.3
Zenobia pulverulenta (Bartr.) Pollard	...	...	....	12	0.4	6.3

[1] Grateful acknowledgment is made for funds and personnel services made available by the Riegel Paper Corporation. The data presented herein were collected as part of a co-operative wetland study project sponsored by the Riegel Corporation and the School of Forestry, Duke University.

shrub classes have been combined. Author citations for plant names are given in Table I. Each species is characterized by its density (d), representing the average number of stems per quadrat, and its frequency (f), the percentage of quadrats in which it occurred.

Results

Among the five most abundant species for each site, *Lyonia lucida, Clethra alnifolia* and *Smilax laurifolia* are common to both, with the first two much stronger under drier conditions and smilax much preferring the wetter site. The data for *Cyrilla racemiflora* clearly substantiate the observation of Wells (1928) that, "Perhaps the most striking species change is the increasing dominance of *Cyrilla racemiflora* as the habitat becomes wetter. With the introduction of drainage into the community dominated by the latter, the reverse process will ensue and *Ilex* and *Morella* (*Myrica*) become prominent."

Atlantic white cedar (*Chamaecyparis thyoides*), while present in the seedling-shrub strata on both sites, has a much weaker representation on the wetter site; and it drops out of the tree stratum completely on the poorly-drained area (Table II).

Table II. Stem count, density (d), and frequency (f) of tree species on contiguous well-drained and poorly-drained sites. Sixteen 8.33-milacre quadrats were counted on each site. Because no understory stratum (U) could be distinguished on the poorly-drained site, all trees there over 12 ft. tall have been classed as overstory (O)

		Well Drained Site			Poorly-Drained Site		
Species	Stratum	Total stems	d	f	Total stems	d	f
Acer rubrum	O	29	1.8	81.3	16	1.0	50.0
	U	83	5.2	93.8	..	...	....
Chamaecyparis thyoides	O	2	0.1	12.5	..	...	....
	U	26	1.6	68.8	..	...	....
Cyrilla racemiflora	U	82	5.1	93.8	..	...	....
Ilex coriacea	U	4	0.3	18.8	..	...	....
I. myrtifolia	U	5	0.3	25.0	..	...	....
I. vomitoria	U	5	0.3	6.3	..	...	....
Liriodendron tulipifera	U	1	0.1	6.3	..	...	....
Magnolia virginiana	O	..	...	.....	1	0.1	6.3
	U	18	1.1	56.3	..	...	....
Nyssa sylvatica var. *biflora*	O	1	0.1	6.3	25	1.6	56.3
	U	69	4.3	100.0	..	...	....
Persea Borbonia	U	5	0.3	25.0	..	...	....
Pinus serotina	O	66	4.1	100.0	54	3.4	93.8
	U	17	1.1	68.8	..	...	....

Swamp gum (*Nyssa sylvatica* var. *biflora*) prefers the wetter site as a seedling, but does much better as a sub-dominant tree on the drier site. With the exception of pond pine, swamp gum is the only tree species which has a frequency of 100%.

Pond pine is unquestionably the dominant tree species on both sites. The data in Table II clearly indicate that it has benefited remarkably from drainage; but they somewhat belie the stunted, depauperate habit which the pine assumes on the wet site (Fig. 1). The poorly-drained site supports dominant trees 20-25 ft. tall, while those on the drier site reach 40-45 ft. in height. Comparative basal area, and average d.b.h. data (Table III), further indicate the influence of drainage

Fig. 1. The pocosin type vegetation on the poorly-drained site, showing the depauperate pond pine above the dense, 10-ft. high shrub union.

Table III. A comparison of basal area per acre and average diameter at breast height on adjoining well-drained and poorly-drained sites. Because on the wet site no understory stratum (U) could be distinguished, all trees there over 12 ft. tall have been classed as overstory (O)

		Well Drained Site		Poorly-Drained Site	
Species	Stratum	B.A./acre (ft^2)	Ave. dbh (in.)	B.A./acre (ft^2)	Ave. dbh (in.)
Pinus serotina	O	71.03	5.1	39.61	4.2
	U	5.97	2.9	.....	...
Acer rubrum	O	14.78	3.5	1.73	1.6
	U	8.85	1.6	.....	...
Nyssa sylvatica var. *biflora*	O	.18	2.1	2.35	1.6
	U	7.06	1.6	.....	...
Magnolia virginiana	O	.....	...	.05	1.0
	U	1.55	1.4	.....	...
Chamaecyparis thyoides	O	2.93	6.0	.....	..
	U	5.12	2.2	.....	...
Cyrilla racemiflora	U	8.26	1.6	.....	...

on the development of the pine, still at approximately one-third of its mature age (Kaufman, et al., 1954). The successional role of pond pine in this situation is indicated by its complete absence from the seedling and transgressive strata on the better site, despite its frequency of 100% as an overstory tree, and 68.8% in the understory. This is interesting in the light of its reported shade tolerance as a seedling (Ashe and Pinchot 1897).

Discussion

Immediately apparent upon approaching the area is the difference between the well-stocked pond pine on the well-drained site, and the dense, tangled scrubby pocosin vegetation with scattered, poorly developed pine on the wet site (Fig. 2).

Fig. 2. Pond pine and associated species of the poorly-drained site, left, compare unfavorably with those on the well-drained site to the right. The dragline canal to the right of the road is obscured by shrubs.

Here is a remarkable demonstration of a marked change in the physiognomy of contiguous sites having been triggered by alteration of a single factor of the environmental complex, The forest floor on the well-drained site consists of a thick pine needle-broadleaf litter with an active A_o layer. The work of ants, rodents and other soil organisms is everywhere in evidence in the shade of the moderately tight canopy. This site supports well-defined seedling, shrub and transgressive strata as well as distinct and dominant understory-overstory strata.

On the wet side of the drainage barrier there is a hummocky sphagnum-sedge ground cover, with surface water visible much of the year. Aeration is poor; and the fauna is most conspicuously represented by the cottonmouth. Here the great mass of vegetative growth comprises a tangled ten-foot high shrub union, with the trees which exceed this height scattered and obviously under tension.

That drainage of a wet site can produce marked improvement in the growth of existing trees has been demonstrated by many workers. LeBarron and Neetzel (1942) recorded a 2- to 4-fold acceleration in the growth of arborvitae following shallow drainage of a northern Michigan bog. Maki (1955), comparing well-drained and poorly-drained loblolly pine in southeastern North Carolina, found that, after 17 years, drainage was reflected in more than double height growth, a 14-fold increase in yield per acre, and a near doubling of average d.b.h. There have been reports of a doubling in growth of slash pine in response to drainage (Schlaudt 1955); and Zon and Averell (1930), report the results of drainage studies in Minnesota and Wisconsin where phenomenal growth increases were recorded for black spruce, tamarack, cedar and hardwoods. Coile (1952a) mentions site indexes of over 90 feet at 50 years for pond pine on soil that is not continuously waterlogged; and he finds that height growth is favored by increased amounts of silt and clay in the subsoil. The same author (1952b) presents equations for estimating site quality for pond pine on mineral and organic soils. In Switzerland, Grünig (1955) observed that spruce and pine grew much faster in height and diameter following drainage of moor areas.

The hazards of oxidation, with subsequent lowering of surface elevation, and of fire which is exceedingly difficult to control, are stressed by Schlaudt (1955) and militate strongly in favor of controlled water drainage rather than free water drainage in organic soils. The advantages of such control from a silvicultural point of view, even in soils that are not strictly organic in nature, are strongly implied in the literature pertaining to the species considered in this report.

Kaufman and Posey (1953) suggest that, because of the serotinous cones, adequate seed dispersal for pond pine may be dependent upon the properly timed use of fire. Korstian (1924), and Buell and Cain (1943), found that natural establishment of cedar is frequently dependent upon fire, as a natural clearing agent, during periods of high water when the seed-containing surface peat is protected. Alternatively, because pond pine grows faster than cedar, particularly as a seedling, and is more tolerant of fire (Korstian and Brush 1931), it might be expected to succeed cedar where drainage cannot be controlled to provide satisfactory seeding conditions for the cedar.

The influence of the water table is indicated in the pattern of establishment of *Chamaecyparis* on these sites. On the drier site it exists as an understory tree in more than two-thirds of the quad-

rats, and as a seedling or transgressive in nearly one-half of the quadrats. In contrast, it is represented in approximately one-fifth of the wet site quadrats as a seedling, but in no case is it recorded as having reached tree size (i.e., 12 ft. or higher). It is clear that the seed source is present, and, with controlled drainage, cedar could be maintained.

Swamp gum is present as an understory tree in every quadrat on the drier site. It is represented by an occasional individual in the overstory. On the wet site it has reached tree size in more than one-half of the quadrats, and is present as a seedling or transgressive in 78.1% of the quadrats. This species will certainly constitute an important successor to pine on the drier site under existing conditions of drainage.

Red maple (*Acer rubrum*), commercially a weed under these circumstances, cannot be overlooked ecologically. On the drier site it is most important as a component of the overstory and understory strata, and appears in 62.5% of the shrub quadrats. Conversely, on the wet site, red maple appears in only one-half of the tree quadrats, while, as a seedling, it occurs in 81.3% of the quadrats. LeBarron and Neetzel (1942) found that red maple and alder become established after clear cutting of arborvitae followed by drainage. Accordingly it seems inevitable that maple would be a strong associate in the natural succession on both sites in Green Swamp.

Summary

Marked differences in the establishment and growth of pond pine in response to drainage conditions are demonstrated. On the basis of basal area or height, growth on the better drained site is nearly double that on the poorly drained site. The development of pond pine, and associated species, as seedlings, transgressive shrubs, and understory and overstory trees, considered in the light of pertinent literature, indicate that under conditions of controlled drainage, with or without controlled burning, sites such as those considered might be managed for the production of pond pine, Atlantic white cedar or swamp gum.

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EFFECTS OF FIRE ON UNDERGROWTH VEGETATION IN UPLAND SOUTHERN PINE FORESTS

Earl J. Hodgkins

Man has known since prehistoric times that a fire in the forest usually causes a temporary increase in the diversity and growth of vegetation. Recently, it was demonstrated that neolithic farmers in Denmark took advantage of this fact, following a regular pattern of clearing, burning, planting, and abandonment in their mixed-oak forests (Iversen 1956). Burned areas were more fertile than unburned areas, and certain wild species appeared in burned clearings that did not occur in unburned clearings.

Today we think we know the *modus operandi* involved for these phenomena. Such fires cause increased rates of mineralization and nitrification

of soil organic matter, and they relieve the forest seedbed of a smothering mantle of litter. We still have much to learn, however, concerning the exact nature of the vegetational changes that occur under specific conditions. We also have much to learn concerning the durability of vegetational changes after fire and the interrelationships among species as they affect durability of changes. This paper reviews the literature on vegetational changes following fires in upland southern pine forests and reports on changes following experimental burnings in northwestern Alabama at the Fayette Forest Unit of the Agricultural Experiment Station System of the Alabama Polytechnic Institute.

Foresters have experimented with fire as one possible means of controlling an invading undergrowth of hardwoods in stands of loblolly pine and shortleaf pine. Effects of fire on mortality, kill-back, and sprouting of this type of vegetation have been reported. The principal findings seem to be about as follows:

1. Thin-barked species are more susceptible to fire-killing and damage than are thick-barked species. Winter burning in a loblolly pine stand of the Atlantic lower coastal plain readily top-killed all understory southern waxmyrtle, but few hardwoods such as sweetgum were killed back if over 1 inch diameter breast high (Lotti 1956). In Texas, prescribed burning top-killed all thin-barked species up to 3 inches d.b.h. where the pine litter was uniform (Silker 1953).

2. Top-killing of a small hardwood is most effective in killing or weakening the plant if it is done when the plant's carbohydrate reserves are at a minimum. Depletion of carbohydrate reserves in a hardwood continues in the spring until the photosynthetic area of the newly emerging leaves is adequate to maintain growth and other plant functions. Maximum accumulation of reserves occurs just before the end of the growing season (Woods 1955). Thus, late spring or early summer fires had the greatest weakening effects on understory hardwoods, and when these fires were repeated annually for 2, 3, and 4 years, they killed the rootstocks of a larger and larger proportion of the hardwoods (Chaiken 1952, Harrington and Stephenson 1955, Lotti 1956). Annual winter burning for 5 years had no effect in diminishing the sprouting ability of repeatedly top-killed hardwoods (Chaiken 1952).

3. Fires in regions of hotter and drier climates may be more effective in killing hardwood rootstocks than fires in regions of cooler and wetter climates. Thus while Lotti (1956) had to use annual summer fires to kill the rootstocks of small hardwoods in eastern North Carolina, Silker (1957), working in the hotter and drier climate of east Texas, killed appreciable numbers of small yaupon, southern waxmyrtle, sweetgum, flowering dogwood, and holly through repeating either winter, spring, or fall burns just once after a 2-year lapse of time. The two investigators burned under similar fuel and weather conditions. Severe drought during the growing season following the first burn may enable one to attain results similar to Silker's where the average climate is normally cooler and wetter.

4. Fires that are hottest near the groundline do the most damage to small hardwoods. In this connection, Lindenmuth and Byram (1948) found that backfires are hotter near the ground than are headfires, although in actual tests in east Texas both types of fire, when applied in the summer, killed 20 per cent of the undergrowth hardwood rootstocks (U. S. Forest Service 1957). In certain heavy mor humus types, single hot groundline fires may kill outright a large proportion of the hardwood rootstocks (Little and Moore 1953). In such cases, high mortality is undoubtedly due to the occurrence of rootstocks partially within the F and H layers of the forest floor rather than wholly within the mineral soil layers. A gentle and steady wind movement during prescribed burning was stipulated by McCulley (1950), by Silker (1953 and 1955), and by Lotti (1956) for the purpose of keeping heat near the ground and away from the crowns of overstory pines.

5. Hotter fires top-kill the larger hardwoods. Summer fires are hotter than winter fires, so generally do more damage to hardwoods. Little and Moore (1953) top-killed with a severe summer burn all of the 1- to 3-inch diameter hardwoods and from one-third to one-half of the 4- to 6-inch diameter hardwoods on both upland and lowland pitch pine-hardwood sites in New Jersey. Lotti (1956) found that winter burning seldom top-killed sweetgum, blackgum, and oaks over 1 inch in diameter; and Chaiken (1949) found that winter burning would top-kill hardwoods only up to 1 or 2 inches in diameter. Little and Moore (1949) used repeated winter fires to kill small hardwoods under 2 feet tall in the pine-oak forests of southern New Jersey.

The over-all heat effect of headfires is apparently greater than that of backfires. Thus, the United States Forest Service (1957) found in the loblolly-shortleaf pine type of east Texas that growing-season headfires killed during any season the tops of more small hardwoods than did backfires. This in no way invalidates Lindenmuth's and Byram's finding (1948) that backfires are hotter at the groundline than headfires with the

result that they should do more damage to rootstocks than headfires.

The heat of a fire, of course, depends upon the fuel type as well as upon the season and type of fire. Logging slash and deep pine litter give the hottest fires. Elliott and Pomeroy (1948) reported that a brisk prescribed winter burn in logging slash top-killed all hardwoods under 1 inch d.b.h. and 86 per cent of the 1- to 4-inch hardwoods in the loblolly pine type of Virginia two months after a clearcutting. Of the hardwoods that were top-killed, 8.4 per cent of the trees under 1 inch and 58 per cent of the trees 1 to 4 inches in diameter did not resprout. Lotti (1956) found that a heavy pine needle rough burned with too much heat for a safe summer fire and had to be first reduced with a winter burn. Hardwood litter burned less readily than pine. Silker (1953) found that fires in uniform pine litter, such as occurs in plantations, were most effective in hardwood killing. Hardwood litter was difficult to burn. Later Silker (1955) reported that prescribed burning in older, partially cut pine-hardwood stands had only a limited effect in killing small hardwoods. Backfires could not be successfully maintained in these stands in the fall of the year, and "strip headfires" had to be used.

6. Any reduction of hardwoods with a single fire is usually temporary, and the net result after a very few years is often an increased coverage of hardwoods. Thus, Brender and Nelson (1954), after cutting and burning a 19 per cent cover of small hardwoods in the Piedmont following clearcutting of the shortlearf pine overstory, found that the reduction in amount and height of shade lasted only 2 years. After 6 years, the amount of hardwood cover in the 1- to 4-foot height class was greater on the burn than on the control. Nine years after an accidental fire in a pure loblolly pine stand in the Duke Forest, Oosting (1944) found that crown fire had changed the type to pine-hardwood and that surface fire had caused a great increase in both numbers and sizes of hardwoods in the understory. In the loblolly pine type of the lower coastal plain of North Carolina, Wenger (1955) compared increase in hardwood cover after clearcutting and burning with normal increase in hardwood cover after clearcutting alone. Burning caused a faster rate of increase on all well-drained soils, but retarded the rate of increase on poorly drained soils with plastic subsoils. The burning influence seemed to last approximately 3 years in both cases. Wenger though that probably increased mineral nutrients and nitrates stimulated growth on the well-drained soils, but that hardwoods on the poorly drained soils suffered from deceased oxygen after fire.

Non-tree vegetation, unlike the hardwood understory, is essentially absent in the undergrowth of well stocked upland pine forests that are completely protected from fire. At the other extreme, frequent burning causes the development and maintenance of a comparatively lush undergrowth of herbs, often with grasses as the dominant species. This principle was well illustrated for the longleaf pine type by the "Roberts Plots" near Urania, Louisiana (Bruce 1947), where 32 years of annual burning, commencing with the 1-year seedling stand, was compared with 32 years of complete protection. Both burned and unburned plots were fully stocked in the pine overstory at the end of the period. The burned plots had a good ground cover of *Andropogon divergens* (Hack.) Anderss. and *A. scoparius* Michx. The unburned plots had no herbaceous understory, but instead had a fair understory of invading hardwoods. The overstory of the unburned plots was dominated by invading loblolly and shortleaf pines. Heyward (1937) found the soils in annually burned longleaf plots to be morphologically closer to grassland soils than to typical forest soils.

Lemon (1949), working in the wiregrass type of the longleaf-slash pine forest, classified the Andropogons and the Panicums as "fire-followers" because they built up in numbers and density following a prescribed winter fire. After a few years, they gradually declined if additional burning was not applied. Andropogons decreased very slowly because of their tillering and rhizomatous habits. Common broomsedge (*A. virginicus* L.) reached its peak density in the second growing season after a fire. Lemon found that various *Compositae* were also important fire-followers, but many of these completely disappeared within eight years after burning. He concluded that the reaction of any one species to fire depended on its morphological adaptations for (a) invading litter-cleared ground after fire and (b) avoiding debilitating damage from the fire itself. The predominant herbs before burning were Curtiss dropseed (*Sporobolus curtissi* (Vasey) Small) and pineland threeawn (*Aristida stricta* Michx.). Because their meristematic tips are more than an inch below the ground surface in winter, the numbers of rootstocks capable of sprouting are essentially unaffected by winter fires. Although they lack the invasive ability of the fire-followers, they tend to regain their original density within a very few years after a single burn because they have the best ability to withstand litter accumulation. It is reasonable to assume that in the absence of these species the Andropogons would maintain

themselves for much longer periods following fire.

After reviewing the literature, Garren (1943) concluded that fire in longleaf pine stands reduced the amount of *Andropogon virginicus* but did not affect the vigor of *A. scoparius*. Severe burning decreased all grasses and increased weeds. Garren was undoubtedly concerned with the effect of frequent and severe fires on grass stands that had already reached their maximum development as the result of previous fires.

The Andropogons appear to be "fire-followers" in other forest types of the Southeast besides the longleaf pine type. Wells (1928), after studying plant communities of the coastal plain of North Carolina, concluded that continued burning of upland oak-hickory might eventually bring about a vegetational type in which Andropogons would be dominant. He classified the upland longleaf and loblolly pine types as consocies of upland oak-hickory subject to the same process; but he placed longleaf pine-turkey oak-*Aristida*, of the coarse sand ridges, in a separate associes little affected by fire under normal xeric conditions. Oosting (1944) investigated the vegetational effects of a crown fire and a surface fire, both in November 1931, in an old-field loblolly pine stand. The stand was 35 years old and on a good site in the Duke Forest. Herbs, including *A. virginicus*, showed a temporary increase after both kinds of fire. Sumacs and blackberries also invaded after both types of fire, and they were apparently more durable than the herbs. However, they were gradually disappearing when measurements were taken nine years later. There was a marked increase in the amount of poison ivy (*Toxicodendron radicans* Ktze.) and Virginia creeper (*Parthenocissus quinquefolia* (L.) Planch.) after surface fire. Japanese honeysuckle (*Lonicera japonica* Thunb.) also was apparently increased by surface fire.

Buell and Cantlon (1953) investigated the vegetational effects of different frequencies of burning, from 1-year to 15-year frequencies, in the oak-pine type on coarse sandy soil in New Jersey. As measured on line intercepts, the cover of herbs increased with the frequency of burning, varying from 0.3 per cent on unburned plots to 5.5 per cent on annually burned plots. Most of the herbaceous growth was contributed by *Andropogon scoparius* and *Carex pensylvanica* Lam.

Stoddard (1935) found that prescribed fires increased both annual and perennial legumes that were important food plants for upland game in open pine stands of the Southeast. Light fires scarified legume seed and hastened its germination. Late winter was the best season for burning, a time neither early enough to cause premature germination nor late enough to destroy already-germinated seedlings. Perennials sprouted and seeded prolifically after fire that occurred even as late as May, and they produced better seed crops as the result of the burning. Garren (1943) cited numerous authorities who found that legumes, as well as *Chrysopsis* spp., increased following fire in grasslands of the longleaf pine type.

Lay (1956) investigated the effects of repeated spring, late summer, and winter burnings on deer forage conditions in loblolly-shortleaf pine stands and in slash pine plantations of east Texas. All burnings reduced browse forage for 2 years and increased herbaceous forage for at least 3 years. Measured on line intercepts, yaupon (*Ilex vomitoria* Ait.), American holly (*Ilex opaca* Ait.), and blackgum (*Nyssa sylvatica* Marsh.) were decreased; cat greenbrier (*Smilax glauca* Walt.), briars (*Rubus* spp.), herbs, and grasses-sedges were increased. The net effect was an improvement of deer forage conditions.

The Fayette Burning Tests

The study reported herein involved the testing of two experimental burning treatments in the Upper Coastal Plain region of Alabama for effects on vegetational undergrowth in the forest. The work was done at the Fayette Forest Unit (Fayette, Alabama) of the Alabama Polytechnic Institute's Agricultural Experiment Station System. The climate can be characterized as hot and moist; average July temperature is 82° F. and average annual precipitation is 55 inches (Hocker 1955). The average number of frost-free days is 231. Topography is strongly hilly. The soils are typical upland red and yellow podzolic soils with sandy loam or loamy sand topsoils and sandy clay loam to heavy clay subsoils.

Description of the plots

The experimental plots were located on old-field areas, many of which had suffered moderate to severe sheet and gully erosion under past cultivation. The vegetative cover consisted of open to dense stands of loblolly pine (*Pinus taeda* L.) and shortleaf pine (*Pinus echinata* Mill.) 20 to 30 years old, with a variable subordinate vegetation of these pines and of hardwood, shrub, vine, grass, and forb species. The principal hardwood tree species were southern red oak (*Quercus falcata* Michx.), black oak (*Q. velutina* Lam.), scarlet oak (*Q. coccinea* Muenchh.), post oak (*Q. stellata* Wangenh.), blackjack oak (*Q. marilandica* Muenchh.), white oak (*Q. alba* L.), mockernut hickory (*Carya tomentosa* Nutt.), pignut hickory (*C. glabra* (Mill.) Sweet), sweetgum (*Liquidambar styraciflua* L.), blackgum (*Nyssa sylvatica* Marsh.), common persimmon (*Diospyros vir-*

giniana L.), flowering dogwood (*Cornus florida* L.), and red maple (*Acer rubrum* L.). The principal shrubs and woody vines were cat greenbrier (*Smilax glauca* Walt.), briars (*Rubus* spp.), muscadine grape (*Vitis rotundifolia* Michx.), littleleaf sensitivebrier (*Schrankia microphylla* (Dryander) Macbr.), Japanese honeysuckle (*Lonicera japonica* Thunb.), Carolina jessamine (*Gelsemium sempervirens* (L.) Ait. f.), and Virginia creeper (*Parthenocissus quinquefolia* L.). The principal grasses were little bluestem (*Andropogon scoparius* Michx.), broomsedge (*A. virginicus* L.), and panic grasses (*Panicum* spp.), with bent-awn plumegrass (*Erianthus contortus* Ell.) and downy oatgrass (*Danthonia sericea* Nutt.) as important secondary species. The forbs were mainly composites and various legumes, with species of *Desmodium, Clitoria, Lespedeza,* and *Galactia* important among the latter. *The* forbs and grasses appeared to be mostly relicts from the earliest successional stages following abandonment of the fields 20 to 40 years prior to the experimental burnings. The undergrowth of pines, shrubs, and woody vines often appeared to have originated as the result of cuttings and fires that were frequent between 1920 and 1943; most of the pine seedlings are known to have followed immediately after an extensive wildlfire in 1943. Hardwood undergrowth, more or less apparent in most of the pine stands, was and is the active manifestation of a strong trend toward an oak-hickory climax of which examples were abundant on interspersed areas that had never been cleared and cultivated.

Treatments

The burning treatments consisted of August burning applied in 1951 and repeated in 1954, January burning applied in 1952 and repeated in 1955, and complete protection from fire. In choosing times for burning, no effort was made to obtain contrasts in carbohydrate reserves of perennial vegetation, but rather all effort was concentrated on obtaining maximum contrast in the heat of the burns. All treatments were applied on ridges and on slopes. There were 4 replications and 24 plots. Each plot was an acre in area (147.6 x 295.2 feet) and was surrounded by an isolation strip of 45 feet in width. Burnings were applied on clear days within a few days after substantial rains. The 1951-52 burnings, having 10 years of fuel accumulation, were hotter and caused greater changes than the 1954-55 repeat burnings. The August burnings were hotter than the January burnings and caused greater reduction in the forest floor. All other conditions being equal, fires in pine litter and in dead grass burned more intensively and covered the ground much more completely than did fires in other fuel types. Fires in pure hardwood litter were generally the least intensive and often failed to burn all of the area intended for burning.

Vegetational analysis methods after the 1951-52 burnings

Vegetative cover was measured on line intercepts (Canfield 1941) in June 1954, approximately two and one-half growing seasons after the first burnings. Each rectangular plot was divided into two square subplots, and 100 feet of line intercept, broken into two 50-foot segments, was located mechanically near the center of each subplot. Interception by individual species was measured to the nearest .01 foot on all vegetation no more than 6 feet above the ground. All parts of intercepting woody vegetation were measured, but herbaceous vegetation was measured only where it emerged at the ground line. The number of strata recognized up to 6 feet above ground at individual points along the line was variable, usually 2 or less, rarely more than 3, depending on the number of plant species involved at the time. Intercepting tree vegetation over 6 feet above ground was tallied as a single canopy stratum.

Forb, shrub, and woody vine species were identified from Fernald (1950); occasional species not found in Fernald were identified from Small (1933). Hitchcock (1935) was used in identifying grass species. All names were cross-checked in *Standardized Plant Names* (Kelsey and Dayton, 1942).

In order to obtain adequate samples for statistical analyses, all species measurements for vegetation 6 feet and under in height were grouped within treatment classes according to plant form and, in the case of tree reproduction, subgrouped according to known ecological characteristics of the various species. The plant form groups for this low vegetation were tree reproduction, shrubs and woody vines, grasses, and forbs. Tree vegetation over 6 feet in height was placed in an additional group referred to as overhead canopy. Group and subgroup intercept distances in feet were then converted to cover percentages on the basis of each total line intercept within a treatment class equalling 100 per cent. The forb data from the 1954 measurements proved insufficient for adequate sampling and are not presented in this paper.

Tree reproduction was subgrouped into pines, permanent hardwoods, and other hardwoods. Pines consisted of loblolly pine and shortleaf pine. Permanent hardwoods were the oaks, the hickories, sweetgum, blackgum, and flowering dogwood.

TABLE I. Cover of tree reproduction and overhead canopy (in per cent)

Treatment	Reproduction[1]						Overhead Canopy[5]		Overhead Canopy Plus Hardwood Reproduction	
	Pine[2]		Permanent Hardwood[3]		Other Hardwood[4]					
	Mean	L.S.D.[6]	Mean	L.S.D.[6]	Mean	L.S.D.[6]	Mean	L.S.D.[6]	Mean	L.S.D.[6]
Ridge	1.34	....	11.22	....	10.54	....	64.4	....	86.06	.....
	....	1.41	.....	6.87	.....	5.60	....	11.5	.....	17.85
Slope	1.65	....	11.13	....	10.79	....	69.8	....	91.64	.....
Aug. burn	.40	....	13.96	....	12.10	....	57.2	....	83.24	.....
Jan. burn	.69	1.71	11.10	8.44	13.08	6.84	69.8	14.1	93.96	21.86
Check	3.39	....	8.44	....	6.79	....	74.1	....	89.36	.....

[1]Trees 6 feet and less in height.
[2]Loblolly and shortleaf pines.
[3]Oaks, gums, hickories, and dogwood.
[4]Mainly persimmon, sumacs, and sassafras.
[5]All trees over 6 feet in height.
[6]Least significant difference (5 per cent level).

These were considered to be the principal species apt to endure and increase under protection. Other hardwoods consisted primarily of persimmon, the sumacs, and sassafras, species known to decrease with protection.

Vegetational changes after the 1951-52 burnings

Mortality records made after the 1951-52 burnings showed that August burning had killed 97 per cent of 1-inch (diameter breast high) pines, 60 per cent of 2-inch pines, and 60 per cent of 3-inch pines; and that January burning had killed 41 per cent of 1-inch pines but no 2- or 3-inch pines. Very probably, both burning treatments had killed virtually all pines 6 feet or less in height. The analysis of variance for pine reproduction from the line intercept data showed a highly significant superiority of non-burned plots over burned plots, but there was no significant difference between August burning and January burning (Table I). These results were, of course, to be expected in consideration of the non-sprouting nature of loblolly pine. The pine analysis is included at this point to serve as a rough indication of the sensitivity of the hardwood reproduction analyses.

The August 1951 burnings had top-killed the following percentages of permanent hardwoods: 62 per cent of 1-inch trees, 52 per cent of 2-inch trees, and 38 per cent of 3-inch trees. The January 1952 burnings had top-killed 46, 5, and 0 per cent, respectively, of these size classes of permanent hardwoods. By June 1954, however, reproduction of both permanent hardwoods and other hardwoods was more dense on all the burned plots than on the non-burned plots. However, none of the differences were statistically significant (Table I). It can be said, therefore, that new hardwood growth had at least replaced all of the original growth up to 6 feet in height killed back by the 1951-52 fires. The new growth was observed to be predominantly of sprout origin, and it often gave the impression in the field that it had

FIG. 1. View in a ridge plot before the prescribed burning of August 1951. Density of the pine overstory was very low in this plot.

FIG. 2. Same view as Fig. 1. Taken in the early spring following the fire.

FIG. 3. Same view as Figs 1 and 2. Taken 3 years after the fire. Cover is reduced in height but not in density. The shrubby vine in the center foreground is *Smilax glauca*.

come back "thicker than ever" (Figures 1 to 3). This heavy resurgence of hardwood sprouts after single fires on upland soils is in agreement with the reports of Brender and Nelson (1954), Oosting (1944), and Wenger (1955) in other areas.

In the analysis for overhead canopy (Table I), fire effects gave an F ratio indicating a probability of 94 per cent that different populations were involved. Individual tests of burning vs. non-burning and August burning vs. January burning gave significance only at the 10 per cent level. The unconventional test of August burning vs. the two other burning treatments combined produced an F ratio indicating a probability of 98 per cent that different populations were involved. This test was accepted as valid in this case since it was known that the August burnings took a rather heavy toll of sapling-size trees. January burnings took such a light toll that normal crown closure may have cancelled their effect by the time the line intercept tallies were made.

In order to test for the possibility of reduction in overall hardwood cover through burning, the data for permanent hardwood reproduction, other hardwood reproduction, and overhead canopy were combined and analyzed. The differences among the means for fire treatments fell far short of significance at any conceivably acceptable level (Table I). Thus it would appear that, in the course of two and one-half growing seasons, the growth of new hardwood sprouts not only replaced the cover of hardwood reproduction lost by burning, but also may have replaced canopy cover lost through August burning. The net effect of burning on the total hardwood cover was simply a reduction of its average height.

Topographic position had no significant effect on any of the classes of tree vegetation (Table I) and did not interact significantly with the burning treatments.

For shrubs and vines and for grasses, negative correlations with tree canopy plus hardwood reproduction were evident from scatter diagrams. This combination factor, therefore, was used in covariance analyses (Federer 1955) for these two classes of non-tree vegetation. Regression of the combination factor with shrub and vine cover was significant; regression with grass cover was highly significant.

In the analysis of variance for per cent of shrub and woody vine cover, all burned plots combined had a highly significant superiority over non-burned plots before adjustment for tree cover and showed a significant superiority after adjustment (Table II). January-burned plots were

TABLE II. Shrub and vine cover (in per cent)

Treatment	NOT ADJUSTED		ADJUSTED[1]	
	Mean	L.S.D.[2]	Mean	L.S.D.[2]
Ridge	10.11	....	9.66	....
	.....	5.30	.....	4.52
Slope	13.41	....	13.88	....
August burn	10.91	....	9.72	....
January burn	18.37	6.48	18.61	5.66
Check	5.96	....	6.91	....

[1]For relationship with tree canopy plus hardwood reproduction.
[2]Least significant difference (5 per cent level).

significantly superior to August-burned plots both before and after adjustment. Thus, it would appear that, while shrub and vine cover is associated negatively with tree cover, it also increases after burning independently of reduced tree cover. The effect is connected with reduction of the forest floor and perhaps with fire-scarification of seed and attractiveness of burned areas to seed-carrying wildlife. The lesser increase after August burning may have been the result of frost-killing of succulent sprouts after the fires,[1] destruction of unripe seed, premature scarification or destruction of ripe seed in the duff, or perhaps to other reasons. Stimulation of shrubs and vines by fire was reported by Oosting (1944) on the Piedmont, but no precedent has been found for the greater stimulation of January burning over August burning.

After adjustment for tree cover, slope plots showed a superiority of shrub and vine cover over ridge plots that barely failed significance at the

[1] Observations for sprouting were not made after the August 1951 fires. After the August 1954 fires, sprouts were very abundant. Many of the succulent sumac and greenbrier sprouts were from 2 to 3 feet long within a month after the fires, and oak sprouts were often 1 to 2 feet high.

5 per cent level (Table II). However, there was no evidence of interaction between topographic position and the burning treatments in their effects on this class of vegetation.

Analysis of the grass data from the line intercepts gave no significant differences either before or after adjustment for tree cover (Table III).

TABLE III. Grass cover (in per cent)

Treatment	NOT ADJUSTED		ADJUSTED[1]	
	Mean	L.S.D.[2]	Mean	L.S.D.[2]
Ridge	1.72	....	1.43	....
	....	2.11	....	1.56
Slope	1.97	....	2.26	....
August burn	2.87	....	2.07	....
January burn	1.64	2.59	1.80	1.96
Check	1.02	....	1.66	....

[1]For relationship with tree canopy plus hardwood reproduction.
[2]Least significant difference (5 per cent level).

The major grass species involved are bunch grasses that have little ability to compete with woody plants on Coastal Plain soils with heavy subsoils. In consideration of this fact and of the highly significant negative regression of grass cover with tree cover, it seems certain that grass, as measured at the groundline level, will in the long run act only in taking up the slack in places where tree and other woody cover has been eliminated.

Vegetational analysis methods and results following the 1954-55 burnings

In a spring, 1955 study conducted by Moore (1956), a 50-foot line intercept was located at random in each of the Fayette plots. In contrast with the earlier used practice of measuring herbs only where they emerged from the ground, Moore measured total interception on the herbs as well as on the woody plants. Two strata were recognized, a grass-forb stratum and an overstory stratum. Moore's survey followed the second burnings (August 1954 and January 1955) by approximately half a growing season. His results contain some cumulative effects of both series of burnings and, possibly, some highly temporary effects of only the last burnings.

Moore's study brought out that both burning treatments favored legumes, composites, and euphorbs (Table IV). Many of the species of these groups are hardy and prolific invaders. Many seed that were undoubtedly already present in the moist lower duff responded to release from the dead litter of woody plants and grasses. Leguminous seed often receive scarification necessary for germination from fire (Stoddard 1935).

TABLE IV. Statistical results obtained by Moore (1956) in his spring, 1955, vegetative survey[1]

Plant Group	FIRE VS. NO FIRE		AUG. VS. JAN. BURN		RIDGE VS. SLOPE		INTERACTION
	F[2]	O	A	J	R	S	F x T
Desmodium	..	..	*	..	..	..	..
Lespedeza	*	..	..	..	..	..	..
Galactia volubilis	*	..	..	*	..	..	..
Euphorbs	*	..	..	..	..	..	..
Compositae	**	..	*	..	..	..	..
Pine seedlings	..	*	..	..	..	..	..
Smilax glauca	..	..	..	..	..	*	..
Andropogons	..	..	..	..	..	*	..
Andropogons adj.[3]	..	*	..	..	..	**	*
Canopy	..	*	..	..	..	..	..
Space	..	..	**	..	*	..	..

[1]*indicates significance at the 5 per cent level; **indicates significance at the 1 per cent level. Asterisks are placed under the treatments which showed superiority.
[2]Legend for treatments: F-fire, O-no fire, A-Aug. burn, J-Jan. burn, R-ridge, S-slope, T-topography.
[3]Adjusted for linear relationship with canopy.

Smilax glauca was shown as unaffected by fire and as more abundant on slopes than on ridges (Table IV). This was the principal species in the writer's shrubs and vines category, which showed a highly significant superiority on burned plots as compared with check plots (Table IV). It is, of course, entirely possible that species other than *Smilax glauca* in the category caused the superiority. It is more than likely, however, that *Smilax glauca* and similar species were superior on the burned plots previous to the 1954-55 fires, that they received a temporary setback as the result of the fires, and that they will again show even greater stimulation after one or two full growing seasons. Lay (1956), in East Texas, demonstrated that *Smilax glauca* was increased in density by both once-repeated and twice-repeated burns.

Andropogons were shown by Moore as of higher density on slopes and ridges and, after adjustment for canopy, as of higher density on non-burned than on burned plots (Table IV). The writer believes that the latter result was due to the time of measurement and represents a temporary tendency toward a forb stage in succession soon to be displaced by stages in which grasses and other higher plants again predominate. According to Bruce (1947), Heyward (1937), Lemon (1949), Wells (1928), and Buell and Cantlon (1953), the Andropogons should increase after burning.

ADDITIONAL DISCUSSION AND CONCLUSIONS

The diversity and growth of herbs and lesser woody species will temporarily increase after any prescribed fire in upland southern pines (Greene 1935, Lemon 1946, Wahlenberg 1935). Fire increases the fertility of an already physically

favorable seedbed, releases it from the smothering effect of litter, releases it from the shade of perennials whose above-ground portions are killed, and eliminates all competition from perennials whose rootstocks are killed.

The forbs are the first to respond to this situation, particularly the legumes and the composites; but vegetation from the living rootstocks of grasses, vines, shrubs, and trees more than reasserts itself at the expense of the new forbs over a period of approximately three years. Even where such sprouting rootstocks are not present, seedlings of the principal grasses and of the woody species will eventually regain ascendance over the forbs, but much more slowly than would the sprouts.

The principal grasses, such as the Andropogons in the Fayette experiment and pineland threeawn and Curtis dropseed in Lemon's report (1949), appear to gain ascendance over other herbs by virtue of their ability to produce litter and to withstand its accumulation. The Andropogons produce litter to the side that will completely clog spaces between the grass clumps if the clumps are not too far apart. Measured at the ground line, grasses will show a durable increase after fire only where the fire has killed the rootstocks of trees and other woody perennials. On normal sandy topsoils with heavy subsoils, they will probably seldom compete seriously with new seedlings of most trees and shrubs and of such vines as *Smilax glauca*. These can originate in openings between the more widely spaced clumps of grass, then overtop the more closely spaced clumps. Woody species are slow to invade even open stands of Andropogons on some old fields, however, because of poor physical condition of the surface soil due to past erosion.

Shrubs and woody vines as a class will establish themselves after fire in competition with existing trees. They will probably give way only slowly to new tree seedlings. They will be particularly resistant, especially in dense stands, to tree seedlings originating later than the first season after the fire. The stature of their perennial, aerial parts makes them immune to smothering under the litter of overtopping trees, a fact that may at least partially explain their superior competitive ability.

The kill of small hardwoods by fire will depend on species and diameter of trees, season of burning with reference to carbohydrate storage in roots, type of forest humus, heat of fire at the groundline, local climate and weather, and frequency and interval of burning. The heat of fire at the groundline will depend on fuel type and amount, the prescribed weather conditions for burning, the burning technique (headfire or backfire), and the microclimate as affected by local cover and topography. A single reduction of hardwoods by burning is usually temporary in nature and within a few years often results in increased hardwood cover. From the admittedly inadequate work done to date, repeated winter reductions would seem to have no permanent effect except where accomplished in conjunction with abnormally dry climatic or weather conditions. Annual summer burns under good pine canopies will kill hardwood rootstocks, but it seems unlikely that fuel accumulations under open pine or under hardwood canopies will be adequate for annual killing fires.

Plainly, fire as a tool for vegetation control has both definite possibilities and definite limitations in upland southern pine forests. A gentle topography is much more adaptable to its use than is a rough topography because of the lesser soil erosion hazard and because of more uniform conditions of fuel, vegetation, and microclimate. A vegetation that is predominantly pine and grass, or pine alone, is more adaptable to the use of prescribed fire than other vegetational types. In such vegetation, fire can be used to either prevent or to stimulate an incursion of hardwood trees, shrubs, and woody vines; and it can be used to stimulate temporary increases in grass and forb species important to domestic and wild animals. Where undergrowth hardwood trees are small enough to be top-killed by fire, repetitive burning can be used to eliminate their rootstocks and to effect at the same time a lasting increase in grasses and other herbs. However, where undergrowth hardwood trees are too large for top-killing with fire, other means must be found for controlling them. Where smaller hardwood trees, shrubs, and woody vines are ecologically dominant, with grass and overstory pines sparse to absent, it is ordinarily extremely difficult to bring about with the use of fire alone any long-lasting change in vegetational composition. After a hot fire in such a situation (providing a hot fire can be obtained in the first place), sprout growth of the original species will usually attain a density and vigor close to that of the original vegetation before fuel conditions will permit an adequate reburning. If, however, such a fire immediately precedes a good catch of pine seed, there will be a strong tendency toward a pine-hardwood type of vegetation if the pines are protected from subsequent killing by fire.

Summary

Experimental burnings were applied in the loblolly-shortleaf pine type in the Fayette Forest Unit (Fayette, Alabama) of the Agricultural Ex-

periment Station System of the Alabama Polytechnic Institute.

The kill of undergrowth trees was more severe in the first burns than in repeat burns (three years later), in August burns than in January burns, and in pine litter and grass fuels than in other fuels. Pine undergrowth was still reduced on all burned plots two and one-half growing seasons after the first burnings. Hardwood cover under six feet in height was more than replaced on all burned plots by sprout growth after two and one-half seasons, but hardwood sapling canopy was still reduced on August-burned plots.

Burning caused increased cover of shrubs and woody vines after two and one-half seasons, even after adjustment for the effect of reduced total tree cover. January burning stimulated shrubs and vines more than August burning. Various ecological reasons are advanced.

After adjustment for a close negative relationship with total tree cover, grass cover showed reduction in the first growing season after burning, complete recovery after two and one-half seasons.

The forb cover increased in the first growing season after fire, with the composites and some of the legumes responding better to August burning than to January burning. Forb cover decreased in subsequent years as grass and woody cover increased.

Conclusions are based on these results and on a comprehensive review of the literature. The succession pattern of forbs-to-perennial-grasses-to-perennial-woody-species after fire seems to revolve largely around the seeding and sprouting habits of the various species involved, and around the abilities of the various plant forms to develop in size and to avoid smothering under organic litter. Invading shrubs and woody vines offer the most substantial competition to trees because of their abilities in these respects.

Fire as a tool for vegetation control in upland southern pine forests has both definite possibilities and definite limitations. The best possibilities occur where the topography is gentle and where the vegetation is predominantly pine-grass or pine alone.

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A STUDY OF PLANKTON COPEPOD COMMUNITIES IN THE COLUMBIA BASIN, SOUTHEASTERN WASHINGTON[1]

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THE STUDY AREA

Between the Northern Rocky and Cascade Mountains a great lava sheet, of about 250,000 km^2, forms the Columbia Plateau (Fenneman 1931). One area of this plateau in southeastern Washington—south and east of the Columbia River, north of the Snake River, and west of the Palouse Prairie country of easternmost Washington—is the Coulee District. Although the Coulee District is a dissected plateau in its topography, it lies at low elevations and is widely known as the "Columbia Basin." The surface of the plateau in the Basin slopes from northeast to southwest, and elevations decline from 700-760 m in the north to near 100 m msl at its southern tip near Pasco (Bretz 1923). Most of the stream channels, and most of the lakes studied, have in consequence a northeast-southwest orientation.

The Plateau was formed by lava which spread out over the region in successive flows from the Miocene into the Pliocene, burying the underlying topography and forming a sheet, locally more than 1000 m deep, of layered, columnar lava. The great weight of the lava sheet caused some subsidence, bringing the plateau surface down to its present low level in the Basin. During the Pleistocene the windblown, loess soils which still form the hills of the Palouse country and of part of the Basin itself were deposited on top of the plateau surface. Streams from melting glaciers, of the Spokane ice primarily, later flowed south and west across the area, eroding through the loess and into the underlying lava, forming a braided network of stream channels across the Columbia Basin. Disappearance of the glaciers and the streams which had flowed from them left the channels as the dry "coulees" of today, largest and best known of which is Grand Coulee. These channels and canyons with their walls of lava, and the buttes and loess-topped mesas which rise above them, form a most distinctive landscape, the "channeled scablands" of the Columbia Basin (Bretz 1923, 1928). The total area of these scablands is somewhat over 5000 km^2. While natural lakes are absent from the mature topography of the Palouse country and the loess islands in the Basin, the scabland channels contain a large number of smaller lakes and ponds.

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Because of the rain-shadow effect of the Cascade Mountains, climate and vegetation of the area are semi-desert. Annual precipitation values range from approximately 41 cm in the northeastern to 15 cm in the southwestern part of the Basin, generally declining toward the west into the more intense rain-shadow closer to the Cascade Mountains. There is thus a marked climatic gradient within the limits of the Basin, with climates ranging from subhumid at the eastern edge, through semi-arid over most of the area, to arid in the southwest (Thornthwaite 1931). The precipitation regime is maritime, with 64 to 70% of total precipitation falling in the winter months, October through March. The dry summers are a limitation on plant growth in the area (Daubenmire 1942), and result in lowering the levels and drying out of many water bodies by summer evaporation. Temperatures are relatively cool, microthermal by Thornthwaite's (1931) classification (but mesothermal by the classification of Thornthwaite 1948); mean monthly temperatures (Fisher 1941) are from —3 to 0° C for January, 21 to 26° for July. Vegetation of the area has been described by Daubenmire (1942). Prevailing climax communities change toward the west along the climatic gradient: from *Pinus ponderosa* forest in the northeastern corner, and Palouse Prairie (*Festuca idahoensis-Agropyron spicatum* zone) along the eastern edge, through bunchgrass prairie (*Agropyron spicatum-Poa secunda* zone) to sagebrush scrub (*Artemesia tridentata-Agropyron spicatum* zone) in the drier western part. Predominant vegetation in the scabland channels is a sparse grassland, more or less mixed with sagebrush (*Artemesia tridentata*) and somewhat disturbed by grazing; in the eastern channels the grass predominates with scattered sagebrush, but toward the west the sagebrush and other shrubs increase to form the northern desert scrub vegetation of the Grand Coulee and other channels.

Most of the lakes and ponds studied lie in depressions in the basic lava or basalt of the scabland channels. The western part of the area also includes extensive areas of sand dunes with many small ponds (Harris 1954; Johnsgard 1956), represented by Pothole No. 1 of the present study. There are a few lakes (*e.g.* Rock and Falls Lakes) which are relatively deep, with shores of vertical or steeply sloping basalt, and are in most cases oligotrophic. Most of the water bodies are shallow and eutrophic, and the area contains hundreds of the smaller ponds which are locally known as "potholes." The larger lakes with stream outlets and some of the ponds are fresh-water bodies. Most of the potholes lose water only by evaporation, however; and in many of them the accumulation of salts has led to conditions of moderate to intense salinity. Salinity conditions vary widely in a single group of ponds; but there is a general tendency of increasing salinity toward the more arid climates of the western part of the area. The most intensely saline bodies encountered were in the Grand Coulee and toward the southwestern corner of the Basin. In some cases a single chain of lakes lying close together show increasing salinities downward along the coulee; the most notable example of this is the chain in the Grand Coulee from the freshwater Falls, Deep, Park, and Blue Lakes to the saline Lenore and Soap Lakes. In salinity conditions the Columbia Basin resembles arid regions described by Decksbach (1924), Young (1924), Gauthier (1928), Stanković (1931), Hutchinson *et al.* (1932), Naumann (1932: 52-4), Beadle (1932, 1943), Jenkin (1932, 1936), and Hutchinson (1937a, 1937b), and especially semi-arid Saskatchewan as described by Rawson & Moore (1944) and Moore (1952). The large number of water bodies of all degrees of salinity offer a particularly favorable opportunity to study effects of salinity on the life of lakes and ponds.

The Columbia Basin has been a sparsely populated area, but an extensive development program centered on Grand Coulee Dam is now affecting it. An extensive area is to be irrigated, and a whole system of man-made lakes and reservoirs has been developed in the western part of the Basin. Many smaller water bodies have been submerged by these, and a number of bodies sampled for the present study no longer exist as such. The extensive reservoirs are resulting also, through rising ground water levels, in higher water levels and lower salinities in many water bodies not actually submerged (Johnsgard 1956). The lakes of the Grand Coulee area are intensively fished; and increasing recreational use of water bodies and increasing change in the natural life of the area by human exploitation are to be expected with increasing populations. The present study began as one of a series of studies of the biology of the Columbia Basin and the impact of human development upon it, then planned at Washington State College. Its objective was to obtain, through samples from a wide variety of water bodies, some information on limnological conditions in the area as expressed in the group of organisms chosen for study, the plankton copepods.

Methods

Plankton samples were taken from 56 water bodies; of these 40 were chosen for microcrustacean population analysis. The bodies studied

may be grouped in relation to five areas of the Basin. One group (Medical, Willow or Murphy, Silver and Clear Lakes and Clear Lake pothole) were from the northeastern and least arid section of the Basin, near the city of Spokane. Also on the eastern edge of the Coulee District, farther south, were the group near Rock Lake and the town of Ewan (Rock and Ledge Lakes, Rock, North Rock, Crescent, Lily Pad, Grass, Tree, Sunken, and Ewan ponds). To the west of these toward the center of the District, and near the towns of Sprague and Ritzville, were a third group (Sprague or Colville Lake, Cow Lake, and Three-inch, East Twin, Marsh, Pear, Disappointment, and Clear ponds). A fourth group (Falls, Deep, Park, Blue, Lenore, Soap, South Tule, and Alkali Lakes, Yellowhead, North Tule, and Avocet ponds) were in the Grand Coulee in the western part of the Basin; and a fifth (Moses Lake, O'Sullivan, Upper and Lower Crab potholes and Pothole No. 1) were south of this in the area of Moses Lake and the Drumheller channels. Names of ponds have been coined by the authors. Locations and summary descriptions of these water bodies are given by Fairbanks (1950); information essential to the present account is compiled in Tables I and II.

These water bodies were visited three times, in spring, summer, and fall—between late March and early May, in July, and in October or November, 1949. Some of the seasonal ponds could be sampled only once or twice. Ten samples of 15 liters each were taken at different points along the shore of a given water body, at depths of 1 m or a little less, above the level of bottom vegetation, if any, and poured through a net of No. 20 bolting silk. Most of the samples thus represent free-swimming, shallow-water or shore plankton. In the lakes, however, both shore and open water plankton were sampled, the latter with oblique hauls of a Clarke & Bumpus (1950) sampler.

Information on water bodies included water temperatures, turbidity readings with a Secchi disk, alkalinity determinations with an electrometric pH meter, areas determined from maps or direct measurements, and depth soundings. A reversing thermometer was used to determine occurrence of stratification during the July visits; only two bodies (Deep and Clear Lakes) possessed a thermocline at that time. Water samples were taken for total salt concentrations and analyses of 12 elements (Na, K, Ca, B, Mg, P, Fe, Cu, Mo, Mn, Sr, and Ag) which could be determined to parts per million or per billion (milliard) by spetrometric and flame photometric methods (Table II).

Plankton samples were killed and preserved in 70% alcohol and set aside until the copepods had lost the red pigments which characterize many of them in this area. Samples were then concentrated into 25 ml of alcohol by means of a miniature plankton net, and fractions of this plankton concentrate were removed for population counts. Two independent counts from the concentrate were made in each case, the two together representing in most cases one-fifth of the original sample, 30 l of lake water. Copepods were tallied in three age groups, as nauplii, copepodids, and adults; the last were determined to species and recorded by sex. Other zooplankters were tallied: Cladocerans to species or genus (except Chydorinae), rotifers, ostracods, and various miscellaneous groups.

The method of handling these population samples, regarded as highly successful, involved mounting fractions of the plankton concentrate on microscope slides in polyvinyl alcohol (PVA). The sample fraction, usually about 1 ml of the concentrate, was transferred by a large-mouth pipette into a rectangular frame on the slide, excess alcohol removed by a blotter, and 4 or 5 drops of PVA added. Large cover slips were then placed, and the slides were heated over a flame until bubbles were removed from the medium and organisms were cleared by blowing out of the internal organs. The PVA mounting renders microcrustaceans transparent and makes visible the fifth feet of copepods; it thus permits determination of these without individual handling and dissection, when sufficient familiarity with the forms being dealt with has been attained. It also provides a permanent reference mount of an actual population sample, in a form in which most adult microcrustaceans may be determined to species. Only by the use of this method, permitting the tallying by species of thousands of copepods, was the population approach of this study possible.

Relations to Salinity and Ion Gradients

The most challenging problem and greatest deterrent to synecological study of plankton is the combination of temporal instability with spatial irregularity of plankton populations. The samples of the present study cannot offer a complete picture of plankton populations, as might be sought from weekly samples from all parts of a given water body. Populations of microcrustacea are less wildly erratic than are those of some smaller plankters, however; and copepod populations showed in the present study a fair degree of consistency through the three seasonal samples from lakes and larger, permanent ponds. Moreover, the approach toward control of population irregularity in the analysis of data was through

TABLE I. Summary of Water Bodies and Microcrustacean Populations

Water body	Total salts, ppm[1]	Area, in hectares	Seasonal relation[2]	Copepod Populations, Percent of Samples[3]														Adult copepods per liter (excluding Harpacticoids)[4]	Adult Harpacticoids per liter[5]	Total copepods per liter[6]	Total cladocerans per liter[6]	Total microcrustacea per liter[7]
				Epischura nevadensis	Diaptomus sicilis	Diaptomus sanguineus	Diaptomus ashlandi	Diaptomus novamexicanus	Diaptomus shoshone	Diaptomus leptopus	Cyclops bicuspidatus	Cyclops vernalis	Cyclops varicans	Eucyclops agilis	Tropocyclops prasinus	Macrocyclops albidus						
Park Lake Group	*244*			*10*			*54*				*36*			*.4*								*6.1*
Rock Lake	170	860	P				100											.15		1.2	.3	1.5
Deep Lake	235	39	P	37			32				30			.6				3.6	.02	6.8	.8	7.6
Park Lake	265	140	P	.4			44				56							.13		3.4	1.5	4.9
Blue Lake	305	210	P	1			41				58			1				.37		6.4	4.1	10.5
Sprague Lake Group	*397*				*5*			*8*			*81*	*4*		*2*								*45.9*
Falls Lake	230	27	P								88			12				1.6		63.2	13.3	76.5
Silver Lake	1000	86	P								93			6				3.6		37.4	12.2	49.6
Clear Lake pothole	330	.4	T								100							1.0	.1	22.1	.9	23.0
Cow Lake	250	85	P		28			1			71							6.1	.07	32.5	45.2	77.7
Moses Lake	210	2060	P		10			9			81							3.5		44.2	138.4	(182.5)[9]
Sprague Lake	335	735	P					21			79							1.4	.9	5.7	17.0	22.7
Clear Lake	425	97	P					34			66			.1				9.9	.07	47.4	10.9	58.3
Yellowhead pond	(7150)[8]	25	S								67	33						0.9		8.5	5.8	14.2
Lake Lenore Group	*2935*				*97*						*1*	*2*	*.04*	*.1*								*72.5*
South Tule Lake	2350	225	P		91						9							11.0		38.8	14.6	53.4
North Tule pond	1040	25	S		98						2							10.2		16.2	10.0	26.2
Willow Lake	4270	36	S		98						1	1		.3				54.2		78.3	11.4	89.7
Granite Lake	4290	43	P		98						.1			1				65.0		94.3	14.9	109.2
Ewan pond	875	4.4	S		99						.1		.4					81.0		130.1	38.6	168.7
Lake Lenore	12100	963	P		100													16.3		76.8	6.1	82.8
Crescent pond	325	.23	T		100													8.0	1.1	64.0	3.4	67.4
Clear pond	620	2.5	T		100													15.0		42.7	15.1	57.8
Three-Inch pond	1190	48	S		97							3						12.3		43.7	4.0	47.8
Medical Lake	2290	43	P		87							13						18.2	.07	20.7	.9	21.6
O'Sullivan Pond Group	*2256*				*4*					*14*	*3*	*24*	*.3*	*51*		*4*						*175.8*
East Twin pond	415	48	S							65		20				15		10.0		22.0	18.8	40.8
O'Sullivan pothole	8710	1.5	S											100				226.5		302.6	7.8	310.4
Avocet pond	610	1.2	T											100				14.0		43.4	42.8	86.2
Sunken pond	310	1.3	S							18		27		46		9		1.1	.8	11.2	3.0	14.2
Upper Crab pothole	2245	1.5	S		22						17	.3	2	58				38.0		233.9	155.5	389.4
Pothole No. 1	1245	.2	T									100						18.0		57.8	151.7	209.5
Disappointment Group	*781*					*88*			*4*		*4*	*1*	*1*	*.5*		*2*						*13.0*
Disappointment pond	390	.01	T			100												0.4		1.0	.2	1.2
Tree pond	290	2.4	T			91					6			3				3.5	.1	17.9	2.4	20.3
Grass pond	670	.54	T			97			3									10.3	.2	22.5	1.8	24.3
Pear pond	1305	.6	T			94					6							6.4		8.4	5.5	13.9
North Rock pond	1320	.4	T			69				19	12							1.6	.1	4.3	6.3	10.6
Marsh pond	410	14	S			75						5	8			12		4.0		6.2	1.3	7.5
Ledge Pond Group	*400*					*12*			*14*		*27*		*36*	*5*		*6*						*58.0*
Ledge "Lake"	370	200	S			25					15		39	10		11		7.2	.3	21.2	4.5	25.7
Rock pond	430	.8	T						27		39		34					5.1	2.1	24.6	61.8	86.4
Lily Pad pond	155	8.5	S								.6	1			99			14.2	2.0	50.6	20.8	71.4
Soap Lake	38700	340	P																		64.7	64.7
Lower Crab pothole	88030	3.0	S																			(24.0)[7]

[1] Total salt determinations are from July water samples in all cases except vernal ponds.

[2] P=permanent and stable; S=semi-permanent ponds, with fluctuating water level and area; T=temporary or seasonal ponds, dry at the time of the summer or fall samples.

[3] Percentages of "Adult copepods per liter," from which average numbers of adults per liter for a given species may be computed.

[4] Average numbers of adult copepods per liter per sampling visit when plankton samples could be taken.

[5] Average numbers of adults per liter per sampling visit, mostly from spring samples. Most or all Harpacticoids are *Canthocamptus vagus*.

[6] Average numbers of copepods, or cladocerans, of all ages per liter per sampling visit when plankton samples could be taken.

[7] Average numbers per liter of copepods plus cladocerans, excluding small numbers of ostracods and phyllopods. The bracketed figure for Lower Crab pothole, however, is for 6.2 adult and 17.8 immature *Artemia salina* per liter on July 29, 1949.

[8] Value probably in error, excluded from group average.

[9] Excluded from group averages. (Moses Lake as a relatively young, dammed lake, the only artificial body sampled, had a very high plankton productivity at the time of the study.)

comparison of groups of samples from several lakes, to permit some averaging out of time-to-time and lake-to-lake variation. Arrangement in relation to the salinity gradient of a small number of water bodies which are not uniform in other conditions may produce a very deceptive picture. When plankton populations may be averaged in groups of several lakes for each interval of the gradient studied, however, there is some hope of distinguishing effects of salinity from those of water-body size and other factors.

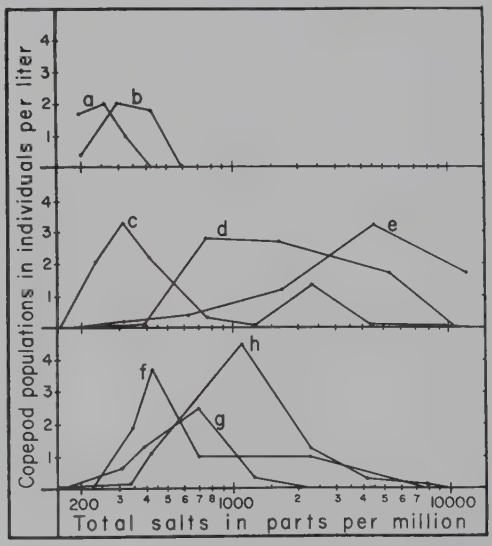


FIG. 1. Distributions of copepod populations in relation to salinity. Points are plotted for average numbers of adult copepod individuals per liter of water per sampling visit, against average total salt contents, for groups of 2 to 6 water bodies. Above: two species of lakes, *Diaptomus ashlandi* (a) and *D. novamexicanus* (b). Middle: three species of both lakes and ponds, *Cyclops bicuspidatus* ×0.5 (c), *Eucyclops agilis* (d), and *Diaptomus sicilis* ×0.1 (e). Below: three species of ponds, *Cyclops varicans* ×10 (f), *Diaptomus sanguineus* (g), and *Cyclops vernalis* (h).

Figure 1 represents the relation to the gradient of total salt concentrations, in parts per million, of species populations expressed as average numbers of adult copepod individuals per liter of water per sampling visit when the lake depression contained water. The groups of water bodies within which populations are averaged include both lakes and ponds for species which occur in both, but include lakes or ponds only for species restricted to one type of water body or the other. The forms of the population figures approximate in some cases a bell-shaped or binominal curve, which has been suggested as the predominant form of population distribution along an environmental gradient (Gause 1930; Whittaker 1951, 1956; Brown & Curtis 1952; *cf.* data of Pennak, 1942, 1951). Use of a linear salinity scale as the horizontal axis results in highly skewed distributions. These become more nearly symmetrical on the log scale of Figure 1, and a "lognormal" relation to the salinity gradient is thus suggested. The manner in which populations relate to a logarithmic gradient further suggests (in analogy with the Weber-Fechner law) that the biological effect of salinity increments is proportional not to absolute magnitudes in parts per million, but to the increment in relation to the salinity to which it is added—$\triangle s/s$.

As may be judged from Figure 1, *Diaptomus ashlandi* is a species of the least saline, oligotrophic lakes; *D. novamexicanus* is a species of eutrophic, fresh to slightly saline lakes. The three species of both lakes and ponds show a sequence along the salinity gradient: *Cyclops bicuspidatus* predominantly in fresh to slightly saline bodies, *Eucyclops agilis* predominantly in mildly to moderately saline bodies, and *D. sicilis* in moderately saline ones. The population of *C. bicuspidatus* shows a second mode in moderately saline bodies. The significance of this is uncertain; but it is of interest that the fresh-water peak of the population is in lakes while the saline peak is in ponds, and it is possible that the two peaks represent two ecotypes within the population of this species. A sequence of sorts appears for the pond species, with *C. varicans* predominantly in fresh to slightly saline, *D. sanguineus* in mildly saline, and *C. vernalis* in moderately saline ponds. The overlaps of these species in relation to salinity are very broad, however, and factors other than salinity seem most critical in determining the presence of one or another in a given pond.

It is consequently impossible to predict the plankton population of a pond from its position on the salinity gradient. For the lakes a clearer sequence appears, but still with considerable irregularity and overlap. Because of this irregularity and overlap, and because the change of populations along the gradient appears to be continuous when groups of water bodies are averaged together, it is difficult to specify particular numbers as limits of fresh-water and saline conditions and of different degrees of salinity. Division between fresh-water and saline bodies at approximately 300 ppm has been suggested by Hesse (1937) and Rawson & Moore (1944). The boundary between fresh-water and saline conditions is presumably to be set where plant and animal populations characteristic of fresh-water conditions are replaced by those characteristic of saline conditions. Apparently

all the copepods of saline conditions in the Columbia Basin occur also in fresh-water conditions there or elsewhere. A distinction between fresh-water and saline communities must consequently be based, not on general distributions of species, but on their distributions and numerical relations within the particular group of water bodies being studied. For copepods of lakes in the Columbia Basin, the fresh-water to saline transition may be marked by change of dominance from *C. bicuspidatus* to *D. sicilis*. The highest salinities in which the former is dominant in lakes are 425 and 1000 ppm, the lowest for the latter 875 and 1040 ppm. No definite boundary between fresh-water and saline copepod communities can be specified, but for most bodies the transition is somewhere between 425 and 875 ppm.

All ponds sampled except one are saline, if a limit of 300 ppm is accepted; but those of lower salinities do not have distinctively saline faunas. No feature as simple as dominance of *D. sicilis* permits characterization of saline ponds and definition of their lower salinity limit; most of the ponds sampled may well be regarded as a single complex of fresh to moderately saline conditions. A distinction may be drawn, however, between fresh-water or slightly saline bodies, with salinities of 310-430 ppm and mixed populations of various combinations of *C. varicans, E. agilis, C. bicuspidatus, C. vernalis, D. leptopus,* and *D. shoshone,* and a group of more distinctly saline bodies, mostly above 410 ppm, in each of which a single copepod species (*D. sicilis, E. agilis, C. vernalis*) was strongly preponderant. All the species involved occurred on both sides of the transitional salinities of about 400-450 ppm, and one pond of 325 ppm contained only *D. sicilis*. A transition, by no means clearly defined, may be suggested, however, between the richer copepod communities of fresh-water or slightly saline ponds below 400-450 ppm and the more restricted and often single-species communities of higher salinities.

Limits in parts per million of fresh-water and saline conditions are clearly variable and indefinite, subject to exceptions in both directions, so far as faunal characterization is concerned, and somewhat different for ponds, with their seasonal intensification of salinity, and for lakes. Limits of salinity classes can in the end only be set arbitrarily, though with regard for what seem to be average salinities at which faunal changes occur. In the Columbia Basin it appears that above 300 ppm a few, above 400-450 ppm the majority, and above 800-1000 ppm almost all, copepod communities are saline in character. The terminology of salinity suggested for the present paper differs from that of Rawson & Moore (1944): 300-450 ppm is regarded as transitional from fresh to slightly saline, 450-1000 ppm as mildly saline, and above 1000 ppm as moderately saline. No upper limit of moderate salinity can be determined from the present data; but Lake Lenore at 12,100 ppm is faunistically in the moderately saline grouping while Soap Lake at 37,800 and Lower Crab pothole at 88,030 ppm have distinctive crustacean communities of high salinities.

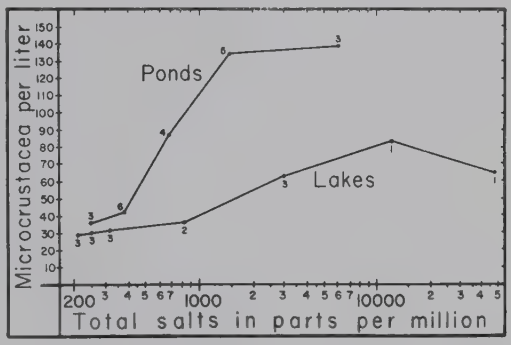


FIG. 2. Standing crops of microcrustaceans in relation to salinity in lakes and in ponds. Points are plotted for average numbers of adult and immature copepods and cladocerans per liter per sampling visit against average total salt contents for groups of water bodies; small figures above and below points are numbers of water bodies averaged.

In Figure 2 microcrustacean standing crops are diagrammed in relation to the salinity gradient. Marked correlations of standing crop, and hence presumably of productivity, with salinity are apparent for both lakes and ponds. Great differences in standing crops appear among water bodies of a given salinity, and in statistical terms the correlation is not high (coefficients of correlation of standing crop *vs.* log salinity of 0.50 for lakes and 0.56 for ponds). It is believed, however, that this means not that the correlation itself is weak, but that standing crops are affected also by many other factors statistical control of which is not possible with the present data. Microcrustacean populations declined at higher salinities from Lake Lenore to Soap Lake, and no microcrustaceans were collected from still more saline Lower Crab pothole. It is unlikely that this limitation of microcrustaceans implies lower productivities at higher salinities in the range sampled. Lower Crab pothole contained a dense population of *Artemia salina* (Table I), and the intense *Artemia* and *Ephydra* production of Great Salt Lake (Hesse 1937) occurs at more than 200,000 ppm.

It is doubtful that the "salinity gradient" has direct, biological meaning to account for its relation to copepod populations and productivity. The salinity gradient may seem little more than a congeries of factor gradients for various ions and

compounds which, however, are complexly intercorrelated and may be variously interrelated in physiological implications. In addition to these chemical gradients there is distinct differentiation of biological communities along the salinity gradient, and consequently differences in characteristics of communities and competitive relations affecting species populations. Taken all together, in both chemical and biological features, the salinity gradient is a "complex-gradient" (Whittaker 1954, 1956), a complex of factor gradients or a gradient of total environmental complexes affecting organisms in biological communities. As such, the salinity gradient may be studied not for any assumption of its direct, causal significance, but only for the significant correlations of chemical and biological characteristics of water bodies which it represents.

It is further indicated by Figure 2 that, on the average, ponds are more productive than lakes at all salinity levels compared. Comparing shore samples for all lakes, with areas over 30 hectares and substantial depths, with ponds of either smaller or shallow basins, average microcrustacean standing crops were 44.5 $\pm$ 8.7 and 80.9 $\pm$ 21.2 individuals per liter per sampling visit (with standard errors of means for 15 and 22 bodies, respectively). Ponds thus supported on the average 1.8 times as dense a microcrustacean population as the shore communities of lakes. A further breakdown compared eutrophic lakes (excluding the Park Group) with larger, permanent and semi-permanent ponds, and smaller, temporary ponds; average numbers of microcrustacea were 58.4 $\pm$ 8.0, 107.2 $\pm$ 37.2, and 39.1 $\pm$ 9.6 for 11, 11, and 10 water bodies. The figures for temporary ponds are for standing crops when there was water to be sampled; they do not reflect the further limitation of annual productivity by disappearance of the aquatic communities during part of the season.

The water analyses (Table II) were obtained to determine whether more direct effects on copepod populations could be established for the various metallic ions, at least. All water bodies were ranked according to content of Na, Mg, K, Ca, B, Mn, Fe, and Cu; and tables were prepared showing the relations of copepod populations to these ion gradients. It is in some cases relatively easy to obtain graphs resembling Figure 1 by suitable grouping of the water bodies, but the significance of such results in questionable. Concentrations of most of the elements studied are correlated with one another and with total salt content; and it is impossible to manipulate the material in such a way as to establish distributional relations to a single element while others and total salts are held constant. Because a given population declines in both directions from its mode along a gradient, this is not a problem to which multiple and partial correlations are suited.

Limited conclusions are possible from inspection of the distributions. An ion whose concentration is more critical in its effect on copepod faunas than total salinity might result in clearer segregation of fresh-water and saline faunas. Sensitivity might be expressed in narrow restriction and insensitivity in broad spread of a species population in relation to a given ion; and relative spread of species along the various ion gradients can be approached as dispersion. None of the ions studied permitted a clearer segregation of fresh-water and saline faunas than did total salt content. For no species was there a clear and unquestionable response of its distribution to a particular metallic ion. There is a suggestion that copper might significantly affect population levels within the range of concentrations represented (0.4 to 212 ppb). High populations of *C. biscuspidatus* and *C. vernalis* were more narrowly confined to the fresh-water end of the gradient (below 4.0 and 4.5 ppb) by copper content than by total salts; high populations of *E. agilis,* in contrast, occurred only in the range of relatively high copper content (17 to 41 ppb). In each case the species population occurred at lower levels along almost the whole range of concentrations represented (highly saline bodies excluded), and it cannot be established that the relation is more than coincidental.

No efforts toward characterizing ponds with different faunas by relative contents of different elements were successful. Ranking of all water bodies by the ratio of Mg to Na (suggested by work of Boone & Baas-Becking 1931) gave striking results: high *D. sicilis* populations occurred only at low values of the ratio (below 0.2), *E. agilis, C. vernalis,* and *D. sanguineus* were concentrated at intermediate values (0.02 to 0.3), and *C. bicuspidatus* at high values (above 0.02). Further scrutiny of the data revealed that, because Na was strongly correlated with total salts and Mg was not, low values of the ratio occurred in saline and high values in fresh to mildly saline bodies. Treatment in terms of the Mg/Na ratio thus simply reproduced the distributional relation of these five species to the salinity gradient and other ions correlated with it. The analysis of Mg/Na ratios may serve mainly to illustrate the perils of unwary interpretation of such material.

Correlation of standing crops with concentrations of various elements is also evident in the data; and coefficients of correlation of standing crop *vs.* log concentration were computed for 9

TABLE II. Concentrations of metallic elements and phosphorus

Water body	Total salts, ppm	Major Elements in Parts Per Million					Minor Elements in Parts Per Billion (10^9)						
		Na	Mg	K	Ca	B	P	Fe	Mo	Cu	Mn	Sr	Ag
Lily Pad pond	155	35	13	6.8	3.2	0.24	115	105	....	5	7	41	..
Rock Lake	170	15	5	4.8	0.7	0.16	141	144	....	9	10	74	19
Moses Lake	210	40	11	11.2	1.8	1.12	....	40	2	1	0.5	195	..
Falls Lake	230	34	15	6.4	1.6	1.04	....	37	0.2	1	2	....	..
Deep Lake	235	26	11	7.6	1.4	0.64	....	17	2	4	4	....	..
Cow Lake	250	26	13	12.0	2.6	0.21	....	32	....	11	15	16	..
Park Lake	265	48	13	11.0	2.3	0.87	..	84	....	5	4	....	..
Tree pond	290	45	22	24.8	2.0	0.29	383	290	....	33	19	59	29
Blue Lake	305	70	24	13.2	4.0	0.85	....	50	3	5	2	....	..
Sunken pond	310	49	6	22.8	2.0	1.13	98	101	....	25	3	19	..
Crescent pond	325	21	10	6.6	2.6	0.50	....	46	....	12	17	227	..
Clear Lake pothole	330	46	27	5.0	3.4	0.68	155	251	3	15	4	50	18
Sprague Lake	335	24	19	9.4	1.4	0.29	....	70	....	4	0.8	253	..
Ledge "Lake"	370	66	28	18.0	2.7	0.05	207	133	....	17	3	....	..
Disappointment pond	390	59	26	61.0	2.8	0.72	....	15	....	13	...	26	..
Marsh pond	410	33	11	8.6	3.9	0.09	....	150	....	0.4	3	....	..
East Twin pond	415	96	32	15.2	2.8	0.20	....	67	....	4	15	25	..
Clear Lake	425	94	7	21.2	6.3	0.08	....	21	....	1	0.5	....	..
Rock pond	430	130	3	32.0	5.3	0.28	....	....	....	5	4	....	..
Avocet pond	610	126	34	19.2	9.0	1.07	226	390	14	18	5	451	..
Clear pond	620	126	23	55.2	5.4	0.35	....	9	....	0.6	8	....	..
Grass pond	670	200	29	33.8	7.6	0.72	....	78	1109	112	3	315	..
Ewan pond	875	302	15	42.4	11.4	0.41	384	416	9	33	9	301	3
Silver Lake	1000	(61)[1]	94	22.0	4.9	1.95	318	750	....	10	85	....	..
North Tule pond	1040	268	14	29.6	12.2	1.85	1529	578	21	11	36	....	..
Three-Inch pond	1190	166	21	35.0	7.2	3.13	1547	595	4	113	...	....	..
Pothole No. 1	1245	224	66	131.0	12.4	1.86	....	234	....	2	93	....	..
Pear pond	1305	365	16	124.0	16.0	0.38	....	37	....	4	39	....	..
North Rock pond	1320	84	63	18.8	6.4	4.28	1611	1320	16	32	125	1016	..
Upper Crab pothole	2245	(2070)[1]	56	192.0	48.0	0.53	....	10	27	41	...	....	..
Medical Lake	2290	715	10	54.0	30.0	0.76	....	55	....	2	2	....	..
South Tule Lake	2350	705	10	122.0	28.0	1.64	....	336	63	212	11	....	..
Willow Lake	4270	1480	6	210.0	57.0	0.63	....	54	83	4	5	....	..
Granite Lake	4290	1480	7	169.0	28.0	1.60	....	81	....	15	4	....	..
Yellowhead pond	(7150)[1]	202	1	23.0	8.5	1.57	214	242	15	17	31	....	..
O'Sullivan pothole	8710	2600	283	210.0	98.0	3.70	....	113	118	20	...	....	..
Lake Lenore	12100	4140	38	364.0	148.0	9.07	....	181	81	200	...	....	..
Soap Lake	38700	13000	22	1190.0	470.0	8.28	....	390	....	49	...	....	..
Lower Crab pothole	88030	27500	599	1105.0	870.0	24.7	....	1101	1207	194	...	....	..

[1]Value probably in error.

elements in lakes, in ponds, and in all water bodies together. The coefficients for Na (0.50 for lakes, 0.53 for ponds, 0.36 for both together) were almost identical with those for total salts. Positive coefficients of 0.3 to 0.7 were obtained also for K, Ca, Cu, Mg, and B *vs.* standing crops of ponds, for B *vs.* standing crops of lakes; lower and probably non-significant correlations were obtained for K, Ca, Cu, and Mg in lakes and for Fe, Mn, and P in all water bodies. Although significant correlations of standing crops with concentrations of various elements occur in these lakes, causal meaning is hardly to be assumed for most of them. The salinity gradient reflects the accumulation in water bodies of many substances, of which some are among the factors influencing productivity; concentrations of most of these substances are consequently correlated with total salts and with standing crops whether or not they influence productivity. No metal showed evident effect in limiting microcrustacean populations at high concentrations. Two of the most highly productive ponds (O'Sullivan and Upper Crab) were among bodies with highest concentrations of almost all ions studied (excluding lakes of intense salinity); and these suggest that microcrustacean productivities were not limited by concentrations of 2900 ppm for Na, 283 ppm for Mg, 210 ppm for K, 98 ppm for Ca, 4 ppm for B, and 41 ppb for Cu.

Extreme sensitivities to certain ions have been shown for phytoplankton species (Rodhe 1948). The attempts to establish effects of metallic ions on copepod populations were, however, consistently inconclusive. To the extent that conclusions may be drawn from them, these conclusions (except for the circumstantial suggestion that copper might be significant) are negative.

Community-Types and Their Relations

The first attempts to group plankton samples into community-types were based on the salinity gradient and the contrast of lakes and ponds. A sequence of lake types in relation to salinity may, in fact, be recognized. No comparable series of pond types could be established by simple inspection of the data, however; and an alternative approach to classification was explored: grouping of water bodies by measurement of relative similarities of their plankton communities into community-types, which could then be compared with one another and given limnological characterization.

The techniques employed have been developed by ecologists studying terrestrial communities—by phytosociologists (Kulczyński 1928; Motyka 1947; Motyka *et al.* 1950; Matuszkiewicz 1948, 1950, 1952; Sørensen 1948; Poore 1955; Culberson 1955; Bray 1956; Koch 1957), and by animal ecologists (Renkonen 1938, 1944; Agrell 1941, 1945; Forsslund 1945; Brink & Wingstrand 1949; Kontkanen 1950a; Odum 1950; Whittaker 1952), most of whom are Continental students of the "biocenotics" of terrestrial arthropod communities. Two basic types of measurement are used in such work (Williams 1944, 1949 and Hughes & Lindley 1955, have suggested other possibilities; see also Goodall 1952). The *coefficient of community*, originally used by Jaccard (1902, 1908, 1912, 1932) measures the percentage of species shared by two community samples, community-types, or floristic lists among the total number of species represented in one or both:

$$CC = \frac{c}{a + b - c},$$ in which a is the number of species in the first sample, b in the second sample, and c the number of species occurring in both. Other means of measurement modify the coefficient of community to compare samples in terms of relative abundance or importance of species—by frequencies or constancies in the case of plants (Kulczyński 1928; Gleason 1920; Tüxen & Ellenberg 1937; Raabe 1952). The most widely used measurement for animal communities compares them by numbers of individuals of species, within the group being studied:

$$PS_c = 100 - .5\Sigma|a - b| = \Sigma \min (a, b),$$

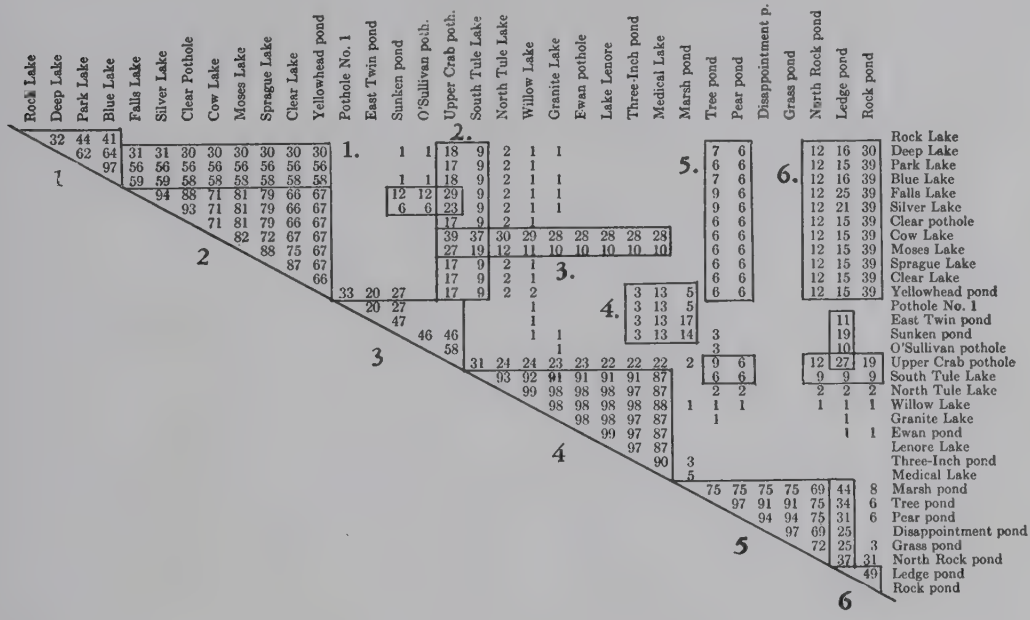
in which a and b are, for a given species, the percentages of samples A and B which that species represents. This measurement, some properties and limitations of which were discussed by Whittaker (1952), has been variously named, but may perhaps best be termed *percentage similarity* of community samples. An alternative to these quantitative approaches has been developed among students of biocenotics in central and southern Europe, who consider that grouping of samples by the non-quantitative techniques of *diagnostic species* (see below) is more effective (Kühnelt 1943a, 1943b, 1951a, 1951b; Rabeler 1947; Gisin 1947, 1951; Franz 1943, 1950; Tischler 1951; Strenzke 1952; Quézel & Verdier 1953; see also Brundin, 1934, and reviews of Renkonen, 1949, Kontkanen, 1950b, and Schwenke, 1953).

Of the two quantitative approaches, coefficient of community measures relative similarity in terms of species composition, and may over-value minor species to the neglect of differences in dominance and major species. Percentage similarity, on the other hand, measures relative similarity of numerical composition in terms of species populations and generally leads to grouping of communities by dominants or major species. It may thus overvalue the sharing of dominant species to the neglect of differences in over-all community composition. Each measurement has its advantages and limitations under different ecological conditions, and use of both for comparison or their combination may often be appropriate. Kontkanen (1950a) has applied both to insect samples and concluded that coefficient of community gave the more effective grouping. The contrary conclusion was reached in the present study; the relatively small numbers of species dealt with strongly limits the significance of coefficients of community and requires an approach through numerical comparison.

For the percentage similarity treatment, data for copepod populations were totaled for sample visits and, in the case of lakes, for shore and open-water samples, and converted into percentages of total samples represented by each species (Table I). Direct computation of percentage similarities is then possible through either of two procedures. Comparing Deep and Park Lakes, which share the species *Epischura nevadensis, D. ashlandi,* and *C. bicuspidatus:* $PS_c = 100 - .5\Sigma|a - b| = 100 - .5[\,37 - .4| + |32 - 44| + |30 - 56| + |.6 - 0|\,] = 100 - .5 \times 75.2 = 62.4$. Or, more simply, for all species shared by the two samples, the smaller percentage values may be summed: $PS_c = \Sigma \min (a, b) = .4 + 32 + 30 = 62.4$.

Percentage similarities were thus computed for all possible combinations of samples, $n(n - 1)/2$ computations where n is the number of samples, and entered in a Kulczyński triangle or matrix (Table III). In the first such matrix prepared, high and low similarity values were scattered in such a way as to offer no recognizable grouping of samples. In order to reveal such groupings, the sequence of the samples should be so changed as to

TABLE III. Matrix of percentage similarities of copepod community samples



maneuver high percentage similarity values toward the diagonal of the matrix, so far as possible. One may begin with a sample regarded as "extreme"; in this case the most oligotrophic body, Rock Lake, was chosen. This sample must be followed by another with which it has highest similarity (Deep Lake), and this in turn by a third whose highest similarities are with Deep Lake and another sample, which becomes the fourth, and so on.

By this procedure (and, often, more than one trial arrangement), the high similarity values by which samples are to be grouped may be clustered along the diagonal as in Table III. Six community-types are suggested, and are marked by heavy triangles. This published matrix has been shortened by eliminating from it certain water bodies (Lily Pad pond, Soap Lake, and Lower Crab pothole) which do not share species populations with the other bodies in sufficient numbers to permit significant comparisons. Certain samples which were identical with other samples in their single-species composition could be dropped without loss of information; Avocet, Crescent, and Clear ponds were thus deleted.

If a single environmental gradient accounts for most or all of the variation among samples, these will fit into sequence in the matrix; and the similarity values will decrease rather uniformly from the diagonal toward the upper right corner. It is obvious that the samples of the present study do not form a simple sequence related to, say, the salinity gradient. The multi-directional interrelations of samples and groups are indicated by the boxes of intermediate similarity values which are distant from the diagonal. In the present, relatively simple material, the meaning of these is easily interpreted in terms of species composition. Thus the widespread species *C. bicuspidatus* links together the first two groups (box 1), and links both of these to certain ponds of groups 5 and 6 (boxes 5 and 6). *D. sicilis* links certain eutrophic lakes with the saline bodies of group 4 (box 3), *C. vernalis* links ponds of group 3 with bodies transitional to groups 4 and 5 (box 4); and the meaning of smaller boxes marked can be determined from Table I.

Means of diagramming and visualizing the multi-directional relations indicated by the matrix were sought. Percentage compositions of the six groupings derived from Table III were averaged (Table I). These averages, in turn, were compared by percentage similarities; and a matrix of community-types was prepared. The results are diagrammed as a plexus of community-types in Figure 3. All percentage similarities above 6 are represented by lines whose lengths are scaled to 100-PS_c, percentage differences expressing relative dissimilarities or ecological distances of the groups from one another. These lines may be related to the boxes, and contacts along the diagonal, of Table III; but a given pair of community-

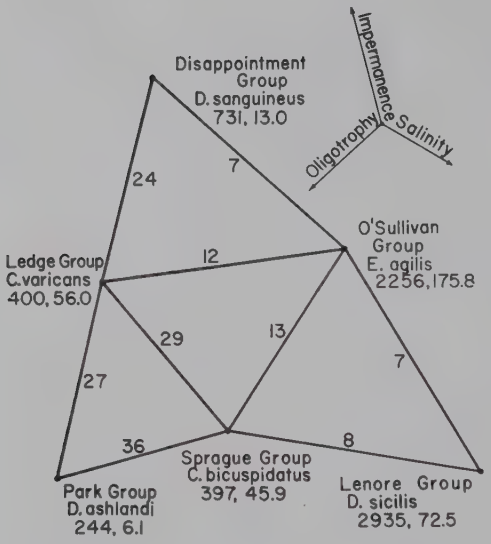


FIG. 3. Plexus of copepod community-types based on measurements of percentage similarity for water-body groupings (see Table I). Percentage similarity values are indicated by the lines; lines are drawn to scale for 100 minus percentage similarity. Information at each point includes a major copepod species by which the community-type may be characterized, average total salt content in ppm (the first number), and average microcrustacean standing crop (the second number) for the water body grouping.

types are generally related by several species. All other relations of community-types, for which no lines are drawn, are expressed in percentage similarities of 6 or less. A generally similar plexus, but with lines of different proportions, results from comparisons by coefficients of community.

The plexus was constructed independently of the authors' interpretations of the environmental relations of these community-types. Its triangular form is contrary to expectation; ecological prepossessions might suggest a square formed by various combinations of fresh-water *vs.* saline and permanent *vs.* temporary conditions. These two gradients are, however, present in the structure of the plexus. The base line from the Park Group to the Lenore Group is in part a salinity gradient; the Park Group are lakes which are both oligotrophic and of low salinity; the Sprague Group is predominantly of eutrophic fresh-water to slightly saline lakes, the Lenore Group predominantly of moderately saline bodies. The larger numbers entered by the names of groups are average total salt contents in parts per million. The vertical axis is, on the whole, but with considerable overlap between groups, one of seasonal regime. The Park Group consists wholly, and the Sprague and Lenore Groups predominantly, of lakes. The Disappointment Group at the upper apex consists of temporary ponds, with one shallow semi-permanent pond (Marsh). The intermediate groups, Ledge and O'Sullivan, include no lakes and are predominantly of semi-permanent ponds—bodies which did not dry during the season of observation but showed marked decrease in depth and area during the summer and fall. Such bodies may dry up in some years, and they subject their communities to greater fluctuations of salinity and other environmental conditions than truly permanent lakes and ponds. (Ewan pond, regarded as a typical "pothole" of this group, showed effects of reduced water volume in salinities of 645, 875, and 1660 ppm in April, July, and October). The plexus thus supports a three-part classification into permanent, semi-permanent, and temporary bodies (*cf.* Gajl 1925 and Decksbach 1929, eustatic, perennial astatic, and temporary astatic).

The plexus represents, not four combinations of salinity and seasonal regime, but three environmental extremes—oligotrophy, salinity, and seasonal instability—and the Ledge, Sprague, and O'Sullivan groups represent various intermediates to these extremes. Relations of these conditions to standing crops of microcrustaceans are indicated by the smaller numbers entered by the groups, averages of microcrustacean populations per liter. Increasing populations toward more saline conditions are indicated for the lakes and suggested for the semi-permanent ponds. Populations of semi-permanent ponds are higher than those of lakes at a given salinity, but temporary ponds have lower populations than either. Both oligotrophy and greatest seasonal instability are reflected in low standing crops; but high salinity, within the range of water bodies represented, is not. The results thus support, from a different grouping of samples and with statistically less effective comparisons, those already discussed.

The community-types may be characterized by species composition as well as limnological conditions (Table I); some major species are indicated on the plexus. In most cases percentage similarities lead to grouping by dominant species; thus the Sprague, Lenore, and Disappointment groups are characterized by dominance of *C. bicuspidatus, D. sicilis,* and *D. sanguineus,* respectively. The Park Group, except Rock Lake, is characterized by sharing of dominance by *D. ashlandi* and *C. bicuspidatus.* The two other pond groupings cannot be characterized by any single dominant species; they appear to be relatively heterogeneous groupings in which *E. agilis, C. vernalis,* and *D. leptopus* are major species for the Sunken Group, *C. varicans* with different

combinations of other species for the Ledge Group. It is thus much less easy to generalize about copepod communities of ponds than those of lakes. In general, the smaller the water body, the more is its plankton a shore-plankton community subject to diverse and little-understood influences of shore and bottom properties, and the less easily predicted is the plankton community from knowledge of major water-body characteristics.

It is of interest to compare these results with those which might be obtained by the grouping by diagnostic species which is very widely practiced among Continental phytosociologists and students of biocenotics in southern Europe. Two types of diagnostic species may be distinguished (Braun-Blanquet 1932, 1951): *character-species* (*Charakterarten, Kennarten, Leitarten*) which are largely or wholly restricted to a given community-type, among a group of these being compared, and *differential-species* (*Differentialarten, Trennarten, Scheidearten*) which are usually much more widespread "companions" (*Begleiter*) occurring in many community-types, but are largely or wholly restricted to one of two community-types being compared and may thus serve to distinguish these. All the major species mentioned except *C. bicuspidatus* are character-species for community-types; in most cases a given species characterizes a community-type not only as a dominant (by numerical importance) but also as both character-species (by relative restriction to the type) and constant (by occurrence in most or all of the samples for that type). In addition, *E. nevadensis* becomes a character-species for the Park Group and *D. novamexicanus* for the Sprague Group. No very effective distinctions by differential-species are suggested by the data, except that *C. bicuspidatus* may be treated as a differential-species separating the highly oligotrophic Rock Lake, with its walls of vertical basalt and waters turbid with colloidal clay, from other bodies of the Park Group. For the material studied here, the quantitative approach through dominance and percentage similarities, and the qualitative through diagnostic species, lead to much the same pattern of community groupings. (It cannot be assumed that they will do so under other circumstances.) By the nomenclature which is standardized in phytosociology, the community-types recognized here might be designated either *associations* (defined by character-species) or *sociations* (defined by dominants). Since animals alone, and a single group of these, are in question, they are termed here simply water-body groupings or plankton community-types.

It is felt that these approaches lead to useful and meaningful groupings of water bodies. The groupings overlap extensively in limnological conditions, and this fact must be considered in any interpretation of them. It may be possible in some cases to construct abstract representations like the plexus discussed which have little limnological or biological meaning. Percentage similarity, for example, may give very misleading results if a given species has two ecotypes dominant in two, distantly related, groups of habitats and communities. Experience with other material suggests that the matrix and plexus approach often gives results less clear-cut and easily interpreted than those in the present work. A virtue of these techniques, however, is that they permit grouping of communities by actual similarity in biological characteristics, in relative independence of ecologists' assumptions about how communities ought to relate to one another according to their environments. They may thus sometimes give a better picture of biological relations than one based on environmental characteristics alone, and in the classification and characterization of water bodies they may well supplement more purely limnological considerations.

Distributional Interrelations of Species

Distributional relations of species may also be investigated through the matrix and plexus approach. A larger number of means of measuring the "association" of two species are available to choose from (see also Goodall 1952). Some of these (Forbes 1907, 1925; Shelford 1915; Dice 1945, 1952; Cole 1949, 1957) are based on direct comparison of the number of samples in which two species occur together, in a given sample series, with the number of occurrences together which would be expected by chance. Others employ coefficients of correlation in one form or another (Iljinski & Poselskaja 1929; Stewart & Keller 1936; Tuomikoski 1942, 1948; Cole 1949; Kontkanen 1949; Nash 1950; Goodall 1953, 1954a; de Vries *et al.* 1954; de Vries 1953; Damman & de Vries 1954). Still others are simple expressions of the percentage occurrence together of species in a set of samples (Agrell 1945; Dice 1945, 1952; Whittaker 1952). Distributional associations of plant species have been studied also by Ramensky (1930), Katz (1930), Scheygrond (1932), Iversen (1936, 1954), Matuszkiewicz (1948), Motyka *et al.* (1950), Gardner (1951), Gilbert & Curtis (1953), Hale (1955), Greig-Smith (1952), Bray (1956), and McIntosh (1957), those of animal species by Backlund (1945), Kontkanen (1950a), and Webb (1950).

It is doubtful that correlation in the usual, product-moment, sense is what should be measured in problems like those of the present study

(*cf.* Cole 1949, and Bray 1956). It is further doubtful that measurement should be based on comparison of actual co-occurrence with that expected by chance. If, in a given series of lake samples, species *a* occurs in 20 of the 40 and *b* in 30 of the 40, co-occurrence expected by chance is $\frac{20}{40} \times \frac{30}{40} = \frac{3}{8}$, or 15 lakes. Occurrence together of the two species in 15 lakes is, by this standard, non-association; and occurrence together in 10 is negative association. But occurrence together in 10 or 15 lakes may be a matter not of chance, but of distributional amplitudes in relation to environment; there may be 10 or 15 lakes of the 40 in which environmental conditions permit both species to maintain populations.

It is considered that the relation to be measured is not co-occurrence relative to chance expectation, or product-moment correlation, but *relative distributional overlap*. Figure 4 illustrates two species with distributional curves overlapping along an environmental gradient (*cf.* Fig. 1); community samples are assumed to be evenly spaced along the gradient. Two approaches to measurement are possible: (1) The number of samples in which both occur may be compared with the number in which one or both occur; in effect lengths of the gradient representing overlap and total amplitudes are being compared—$\frac{b-c}{a-d}$. (2) The cross-hatched overlap area may be compared with one-half the total areas of the two curves (without assuming these to be of binomial form). If the area under a given curve is treated as the sum of the heights of lines for samples such as are marked out between *a* and *b* (*i.e.* the relative numbers of individuals of the species taken in samples along the gradient), and the sum of these heights for a given species is 100%, then the relation of the cross-hatched area to the total areas of the curves becomes a percentage. Measurements in terms of means and dispersions are easily conceived, but are thought unsuitable to the kind of material with which ecologists must usually deal.

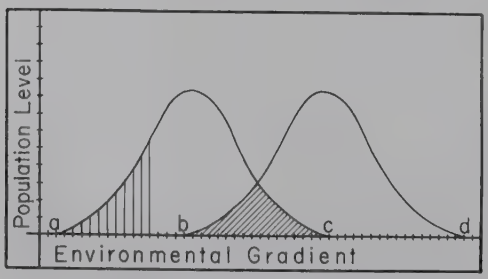


FIG. 4. Distributional overlap of two species in relation to an environmental gradient.

For computation, the first measurement becomes simply the percentage of samples in which both species occur, among samples in which one or both occur: $PC = \frac{c}{a+b-c}$, when *a* is the number of samples containing the first species, *b* the number containing the second, and *c* the number containing both. The most effective means of computing the second measurement is to total the population of a given species in all samples in the series. Numbers of that species in particular samples are then converted to percentages of that total. When all species have been thus treated, a table of percentage distributions corresponding to Table I, but based on vertical computation of totals and percentages, results. From this table the percentage similarities of species distributions may be simply computed for all pairs of species by the same formula as for percentage similarity of community samples.

Of these two measurements the first, which may be termed *percentage co-occurrence,* is analogous to coefficient of community and the second to percentage similarity of community samples. As is the case with the other measurements, they give somewhat different results, and each has its advantages and limitations under different circumstances. Both are, clearly, very strongly influenced by the distribution of samples relative to the total field of occurrence of the species. Rarely are samples taken along a gradient as in Figure 4; often they may be concentrated in the overlap $b - c$ or in one of the non-overlaps $a - b$ and $c - d$. Species populations occur and overlap in relation to many environmental gradients, not one; and rarely can the whole field of occurrence of both be sampled. The measurements cannot in general express the distributional relation of species in the field, only their distributional relation in a particular set of samples. Granting the conspicuous limitations of such measurements, they may still reveal relations of species in samples which are not apparent from simple inspection of tables. As measurements, they are devoid of statistical sophistication, but free also from assumptions about statistical properties of the material and what is to be measured that are embodied in some more formal procedures. For the present, early stage of development of these techniques, they may be preferred as simple and direct expressions of that which an ecologist regards as appropriate to measurement in the distributional relations of species in his samples.

Percentage co-occurrences and percentage similarities of species distributions are given in Table IV. Copepod species occurring in fewer than three water bodies are excluded; distributions of these are discussed in the following section. It is impossible to manipulate the matrices so that all higher values are concentrated along the diagonal, and multi-directional relations among species are indicated by this fact.

TABLE IV. Matrix for relative distributional overlaps of copepod species. Values above the diagonal are percentage co-occurrences, those below are percentage similarities of species distributions. (x = less than 0.5%)

	Epischura nevadensis	Diaptomus ashlandi	Eucyclops agilis	Cyclops bicuspidatus	Diaptomus sicilis	Cyclops vernalis	Macrocyclops albidus	Cyclops varicans	Diaptomus sanguineus	Diaptomus shoshone	Diaptomus novamexicanus
Epischura nevadensis..		75	14	13	..	.	..	..	..	..	..
Diaptomus ashlandi...	29		13	12	..	..	..	..	..	..	..
Eucyclops agilis.....	x	x		40	13	15	13	12	11	..	6
Cyclops bicuspidatus..	4	11	11		29	14	4	17	15	8	17
Diaptomus sicilis.....	..	..	5	6		21	..	12	..	..	13
Cyclops vernalis.....	..	..	3	1	9		27	15	8	..	..
Macrocyclops albidus..	..	..	2	1	..	16		29	22	..	..
Cyclops varicans.....	..	..	30	10	16	2	22		20	14	..
Diaptomus sanguineus.	..	..	1	1	..	1	18	11		25	..
Diaptomus shoshone...	..	..	..	1	..	..	..	21	19		..
Diaptomus novamexicanus.....	..	..	x	58	2	..	...	..	..	..	

Of the two measurements, percentage co-occurrence is regarded as providing the better results in the present material; these values are diagrammed as a plexus in Figure 5. The relations cannot be represented effectively in two dimensions. The heavy *E. agilis-C. bicuspidatus* line should be regarded as an axis from which three plane surfaces radiate outward—*D. ashlandi* and *E. nevadensis* in one direction, *C. vernalis, D. sicilis,* and *D. novamexicanus* in a second, and *Macrocyclops albidus, C. varicans, D. sanguineus,* and *D. shoshone* in a third. *C. bicuspidatus* and *E. agilis* are the most widely distributed species in non-saline and mildly saline water bodies; they are consequently distributionally related to every other species in the plexus (except *E. agilis vs. D. shoshone*). The planes extending outward from the *E. agilis-C. bicuspidatus* axis are formed by species which are characteristic of more distinctive environments. The extreme members of two of the planes, *D. ashlandi* and *E. nevadensis,* and *D. sanguineus* and *D. shoshone,* are almost wholly unrelated to species on the other planes; *C. vernalis* and *D. sicilis* are related, however, to *M. albidus* and *C. varicans,* and these relations are not shown. For the most part, positions toward the center of the plexus are occupied by common and widely distributed or cosmopolitan cyclopids;

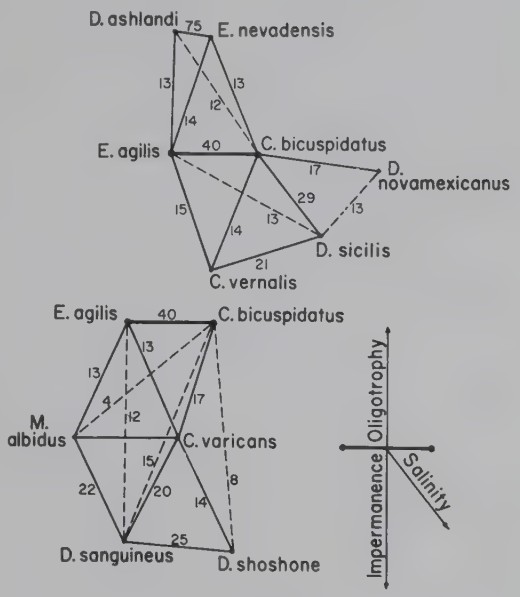


FIG. 5. Plexus of distributional relations of copepod species, based on measurements of percentage co-occurrence (Table IV). Percentage co-occurrence values are indicated by lines connecting species; solid lines are drawn to scale for 100 minus percentage co-occurrence, broken lines are not drawn to scale. The heavy line connecting *E. agilis* and *C. bicuspidatus* is the axis from which radiate three planes for groups of distributionally related species: *D. ashlandi* and *E. nevadensis* in oligotrophic conditions, *C. vernalis and D. sicilis* in saline conditions, *M. albidus, C. varicans, D. sanguineus,* and *D. shoshone* in unstable or temporary ponds.

distal positions are occupied by diaptomids (and the temorid *E. nevadensis*) of more restricted American or western distributions (see also Fig. 3).

Interpretation of the plexus in terms of environmental relations is not difficult. *D. ashlandi* and *E. nevadensis* are the species of oligotrophic lakes, *D. novamexicanus* is a species of eutrophic lakes. *C. vernalis* is a species of slightly to moderately saline ponds, *D. sicilis* a species of saline lakes and ponds. *M. albidus* and *C. varicans* are species of semi-permanent ponds; *D. sanguineus* and *D. shoshone* are species of temporary ponds. The plexus thus represents a central complex of widely distributed species most characteristic of "intermediate" conditions—eutrophic, non-saline, relatively stable water bodies—and radiating from this three planes for species of three types of extreme conditions—oligotrophy, salinity, and seasonal instability. The three planes thus correspond to the three axes of the community-type plexus (Fig. 3).

Distributional Summary

From the preceding and other data, the distribution of zooplankters may be summarized. Nomenclature follows suggestions of Mildred S. Wilson on Diaptomidae, H. C. Yeatman on Cyclopidae, to conform to the forthcoming, new edition of Ward and Whipple (1918); names used in Pennak (1953) are given in parentheses when they differ. Occurrence during all seasons of sampling may be assumed unless otherwise stated.

Cyclops bicuspidatus Claus was the most widely distributed species, occurring in 23 of 40 water bodies with a wide range of ecological conditions—oligotrophic to moderately saline (155 to 4290 ppm), true lakes (both shore and open water) to semi-permanent and temporary ponds, and at all seasons, though maximum population densities were encountered in the spring. It was dominant in many fresh-water lakes and a few saline ponds.

Eucyclops agilis (Koch) was widely distributed with more scattered occurrence (13 water bodies) over the same range of lake and pond conditions. Its population levels were much lower than those of *C. bicuspidatus*—except in certain slightly to moderately saline ponds in which it was dominant. In lakes *E. agilis* occurred in shore samples only.

Diaptomus sicilis Forbes, the third major species, was the principal copepod of a majority of moderately saline bodies (1040 to 12,100 ppm)—both lakes and ponds, and both shore and open waters of lakes—and in some of them was the only copepod. This population of *D. sicilis* (which has been known as *D. natriophilus* Light) is most characteristic of moderately saline conditions; but it was dominant in three ponds in the slight to mild salinity range (325, 620, 875 ppm) and present in two fresh-water lakes (210 and 250 ppm). It was observed in only two temporary ponds; in lakes and semi-permanent ponds it occurred in all seasons, but with densest populations during the fall samples in most cases.

Diaptomus ashlandi Marsh occurred only in the four oligotrophic lakes, and predominantly in open waters of these.

Epischura nevadensis Lillj. was recorded in three of the four oligotrophic lakes, at lower population levels than *D. ashlandi,* also predominantly in open waters.

Diaptomus novamexicanus Herrick (*D. washingtonensis* Marsh) occurred in four eutrophic lakes, in both shore and open waters, associated with *C. bicuspidatus* but at lower population levels than this.

Cyclops vernalis Fischer was the most widely distributed of the species occurring mainly in ponds, collected from 8 of 12 semi-permanent ponds (and in one saline lake and one temporary pond), from fresh-water to moderately saline conditions (155 to 2290 ppm). Although not a species of vernal ponds, it was taken only in the spring in most of these water bodies—but it was recorded also in summer and fall.

Cyclops varicans Sars occurred in four semi-permanent and one temporary pond, slightly to moderately saline (370 to 2245 ppm), and in two of these was a major or dominant species.

Macrocyclops albidus (Jurine) occurred in four semi-permanent, fresh or slightly saline ponds (310 to 415 ppm), in none of which was it the dominant species.

Diaptomus sanguineus Forbes was the major species of temporary ponds; it was the dominant or sole species in six of the 11 temporary ponds studied and occurred in one semi-permanent pond. Like most of the pond species, it occurred over the range from fresh or slightly saline to moderately saline conditions (290 to 1320 ppm). It was collected only in the spring.

Diaptomus shoshone Forbes was the other species of vernal ponds, taken only in the spring from three temporary ponds with salinities from 430 to 1320 ppm. Although occurring at low populations per liter, this species of giants, by the standards of fresh-water copepods, was conspicuous in the plankton wherever it occurred. (Identity of this form is still in doubt; it may be *D. novemdecimus* M. S. Wilson 1953).

Diaptomus leptopus Forbes (= *D. piscinae* Forbes) occurred in only two ponds, 310 and 415 ppm, both semi-permanent; it was the dominant copepod in one.

Tropocyclops prasinus (Fischer) (= *Eucyclops prasinus*) occurred as the dominant species in one strictly non-saline (155 ppm), semi-permanent pond.

Paracyclops fimbriatus (Fischer) was taken in the spring sample from Silver Lake, and *Diaptomus eiseni* Lillj. was taken from Alkali Lake.

Harpacticoid copepods were taken from 14 water bodies, of salinities from 155 to 2290 ppm, in lake shore samples and in semi-permanent and temporary ponds. They were taken in the spring only in most water bodies, and substantial numbers were taken only from shallow ponds. Most, and possibly all, of those tabulated in Table I were *Canthocamptus vagus* (Coker & Morgan).

A considerable number of cladoceran species were recorded in the present study and by Kiser (1939). In general, however, copepods were the predominant microcrustacea. Copepods outnumbered cladocerans by 2.2/1, averaging the whole series of water bodies together, and by a some-

what higher ratio (3.0/1) for 14 lakes excluding Soap Lake. In saline Soap Lake (38,700 ppm) a cladoceran, *Moina hutchinsoni* Brehm, was the sole microcrustacean collected; this species occurred also in Lake Lenore (12,100 ppm) but was outnumbered there by *D. sicilis*.

The samples also included the smaller numbers of ostracods, insects, mites, nematodes, and annelids which enter shore plankton. The most unexpected plankters were the tardigrades which were encountered in three ponds (Rock, Sunken, and Cresecent) and one lake (Cow) and occurred at a population level of slightly more than 1 per liter in Rock pond. The tardigrades from Sunken pond have been determined as *Echiniscus blumi* Richters, those from other bodies as *Macrobiotus macronyx* Dujardin. Rotifers were especially numerous in two saline bodies, Soap Lake and O'Sullivan pothole, but were not abundant in Lake Lenore.

Like other arid and semi-arid areas with many unstable water bodies, the Columbia Basin has a diverse fauna of phyllopods; only a few of these were collected for the present study. *Branchinecta coloradensis* Packard occurred in Willow Lake, and *Eubranchipus serratus* Forbes in Rock pond. The fairy shrimp collected from Alkali Lake, a shallow body of moderate salinity (2180 ppm and pH 9.0) in the Grand Coulee, has recently been described as the new species *Branchinecta mackini* by Dexter (1956). *Lepidurus* sp. was taken from South Tule and Alkali Lakes, where it occurred with *D. sicilis*. *Artemia salina* Leach was the sole crustacean collected from Lower Crab pothole (88,030 ppm) and Soda Lake approximately 100,000 ppm). Conditions of extreme salinity in the Columbia Basin are thus expressed in the crustacean plankton by exclusion of copepods, and single-species communities of other forms—*Moina* in Soap Lake and *Artemia* in some still more intensely saline bodies.

Conclusion

It is possible to treat plankton communities effectively with the procedures of synecology, as distinguished from those of autecology and faunistics. The most formidable problem is that of population irregularity and instability, but this does not preclude synecological research. Comparable problems, if less severe ones, are not unknown in terrestrial communities; they have been observed in such widely different circumstances as tropical rain forest (Aubréville 1938), temperate deciduous forest (Raup 1956), and arctic tundra (Griggs 1934, 1936; Raup 1941). The present study is of limited scale and restricted to a single group of organisms, but may suggest something of what can be done despite the difficulties inherent in plankton synecology.

Much discussion in terrestrial ecology has centered on the nature of community-types—whether these are "real" and natural units, clearly defined in the field and comparable to well-defined species, or are simply produced by ecologists through their classification of the complex and merging patterns of natural communities according to some chosen classificatory criterion (Ramensky 1924, 1930; Gleason 1926, 1939; Lenoble 1927, 1928; Nichols 1929; Raup 1942; Cain 1947; Mason 1947; Whittaker 1951, 1952, 1956; Curtis & McIntosh 1951; Dice 1952; Goodall 1953, 1954b; de Vries *et al.* 1954; Poore 1956). The bases of the latter view were advanced by Ramensky (1924) as two principles: the principle of species individuality—that species are variously and complexly distributed, each according to its own unique physiological and biotic relations to environment and other species, and consequently do not fit into well-defined associations—and the principle of community continuity—that many natural communities intergrade continuously along continuous environmental gradients, so that boundaries between community-types must often be arbitrary.

The material discussed here is not regarded as effective evidence, but it is consistent with the principle of species individuality. Only two of the species had similar distributions (*D. ashlandi* and *E. nevadensis*), and these were not closely similar. What the species-plexus seems to represent is not a number of distinct associations, but a complex pattern of distributional overlaps in which each species has its own, distinctive environmental relation. The treatment of the salinity gradient suggests that, although lakes of similar environmental conditions may have plankton communities sharply different from one another, plankton community-types in general may intergrade continuously along the salinity gradient. The relations of species and community-types to seasonal stability and instability (*cf.* Gajl 1925) suggest that this also may be a complex-gradient in relation to which there is gradation rather than discrete classes of water bodies and communities. The principles of species individuality and community continuity may suggest a very different perspective on what an ecologist is about when he classifies natural communities. They do not imply, however, as some ecologists have felt, that effective study of species interrelation and community classification are impossible.

Geological circumstances of the Columbia Basin have produced a large number of water bodies which will be increasingly used for recreation. Problems of productivity and fish culture are not

a primary concern of this study, but certain conclusions are suggested. Salinity should not constitute a major limitation on fish production in the area. Only a few of the lakes have salinities in excess of the limits for fish production, indicated as about 15,000 ppm by Rawson & Moore (1944). For most of the water bodies the principal limitation is likely to be small size, with its implications of seasonal instability and the possibility of winter oxygen exhaustion under an ice cover in a cool climate. Apart from the minority of strongly saline lakes and the large numbers of seasonal ponds, the water bodies of the Columbia Basin are of relatively high productivities, with their productivities enhanced rather than restricted in conditions of mild and moderate salinity.

Summary

1. The channeled scablands of the Columbia Basin contain numerous lakes and ponds; and many of these, in the semi-arid climate, are saline. Forty water bodies ranging from fresh to highly saline and from true lakes to temporary ponds were selected for study of plankton copepod communities.

2. Population samples of shore and open-water plankton were mounted on slides in polyvinyl alcohol, and adult copepods were tallied by species. The population data made possible an approach which was not simply faunistic, but an experiment in plankton synecology or biocenotics.

3. Relations of species to the salinity gradient were investigated. In lakes *Diapotomus ashlandi* and *Epischura nevadensis* were characteristic of oligotrophic conditions, *Cyclops bicuspidatus* and *D. novamexicanus* of eutrophic fresh to mildly saline conditions, and *D. sicilis* of moderately saline conditions. Pond species were less clearly segregated by salinity and more strongly affected by seasonal instability and other factors. Attempts to establish effects of various metallic ions on species populations and plankton community-types gave inconclusive but generally negative results.

4. Although the area contains deep, rock-walled, oligotrophic lakes, the majority of the water bodies are shallow and eutrophic. Productivity, as expressed in microcrustacean standing crops, increased with increasing salinity in both lakes and ponds through most of the range of salinity conditions sampled. Microcrustacean populations per unit volume of water were almost twice as high in ponds as in lakes, but were low in most of the temporary ponds.

5. A matrix and plexus for plankton samples and community-types were prepared by measurements of percentage similarities; six community-types which could be characterized by copepod populations and limnological conditions resulted. Percentage co-occurrences were used to prepare a matrix and plexus of distributional relations of species. Both treatments suggest a central complex of community-types and species characteristic of eutrophic, fresh to mildly saline, relatively stable water bodies, and community-types and species which depart from these in three directions of environmental extremity—oligotrophy, salinity, and seasonal instability.

6. Distributional relations of copepod species are summarized. Copepods are excluded from water bodies of high salinities; these are characterized by dense populations of single crustacean species (*Moina hutchinsoni* at 38,700 ppm in Soap Lake, *Artemia salina* in still more saline bodies).

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ALTITUDINAL DISTRIBUTION OF SOME ENTOMOSTRACA IN COLORADO

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INTRODUCTION

The state of Colorado holds much interest for the biologist. Portions of five life zones are to be found within the state—Upper Sonoran, Transition, Canadian, Hudsonian and Alpine or Arctic. Each zone has its own climatic, vegetative, and physiographic features, each of which influences the lakes of that zone. In the space of a few miles, here in this region of great altitudinal ranges, occur species which are ordinarily separated by hundreds of miles of latitude. Thus it is possible for the limnologist to sample a plains pond with its lowland fauna in the forenoon and in the afternoon a cirque lake above timberline which contains high latitude or boreal species. Colorado is also a meeting ground of eastern and western fauna as Dodds (1924) has pointed out.

The effect of altitude on the distribution of Entomostraca in this region attracted the attention of such early biologists as Ward (1904), Shantz (1907), and Dodds (1908, 1915, 1917, 1920, and 1924). Beardsley (1902) reported some plains species, whereas Dodd's papers of 1917, 1920, and 1924 were the last dealing exclusively with distribution of Entomostraca in Colorado. Later investigations are of a more broad limnological nature (Pennak 1941, 1945, 1950, 1955a and 1955b, and Olive 1953a and 1954).

It is the purpose of this paper to review the altitudinal distribution of some Entomostraca in Colorado, to consolidate published distributional records for the State, and to report the occurrence of hitherto unrecorded species in Colorado.

METHODS

Collections were accomplished by means of a small Wisconsin plankton net of 173 meshes per inch. In some cases total vertical hauls were made from a boat or raft, in others horizontal tows were made by tossing the net as far out into the lake as possible and then drawing the net to shore. Most of the collections were taken between June and October. The remote locations of many of the lakes precluded more than one trip to each. However, one of the authors (Olive) has carried out a limnological investigation of the Rawah Lakes, a group of sub-alpine and alpine lakes in northern Colorado, and from this work a series of plankton samples was available. A series of plankton-trap collections extending over a full year's time were available from one plains lake, Horsetooth Reservoir. The Colorado Game and Fish Commission kindly loaned plankton collections for examination.

As is well known, the species composition of the plankton within a lake is not constant throughout the year, hence the completeness of single-occasion collections is limited. It is to be expected that further investigations will add more species to the list.

DESCRIPTION OF ZONES

Pennak (1941) defined four limnological zones in Colorado based on altitude and lake typology. There are the plains zone, less than 5,600 feet above sea level; foothills, 5,600 to 8,200 feet; montane, 8,200 to 10,500 feet; and alpine, over 10,500 feet. For purposes of the present paper this zonation is modified to include a sub-alpine zone extending from 9,800 to 10,800 feet.

The alpine lakes of Colorado are to be found along a portion of the Southern Rocky Mountains that extends in a roughly north-south direction through the state. Pleistocene glaciation is responsible for the basin morphometry of the alpine lakes. Many are cirque lakes, filling depressions gouged from solid rock. Others are impounded by moraine dams and still others are the result of both plucking and damming. Meteorological conditions are severe at high elevations and ice cover may persist for nine months of the year. The greatest annual precipitation in the state occurs on the high mountains, some 40 to 50 inches on the average along the continental divide. Pennak (1941, 1945, 1955a) has presented chemical and physical data for selected Colorado alpine lakes. In general this group of lakes may be said to be characterized by low temperatures, low dissolved solids, and low organic content.

The sub-alpine lakes, like the alpine, are found in basins of glacial origin. These lakes are more diversified than the first group, tending to grade into alpine or montane, depending upon the influence of morphometry and local exposure.

Lakes of the montane zone are variable in chemical and physical characteristics as pointed out by Pennak (1945). Most of the natural montane lakes examined in this study are the result of morainal damming, however there are many artificial bodies of water within the montane zone in Colorado. A varied array of habitats for Entomostraca are found in the montane lakes, from near sub-alpine lakes with rocky bottoms to low montane lakes with bottoms rich in organic muck. Total residue ranged from 8.89 to 110.40 mg per liter in 34 montane lakes investigated by Pennak (1941).

The foothills region of Colorado is of unglaciated, well-dissected topography, hence natural lakes are few. All of the foothills lakes referred to in this paper are artificial bodies of water. One, Estes Lake, has recently been investigated by Pennak (1955a).

The lakes of the plains zone differ greatly in chemical nature. Most of these lakes are reservoirs, occupying wind-scooped depressions which are filled by canal systems from mountain water sources. The availability of water for storage in plains reserviors is closely related to the annual precipitation. Some plains lakes have neither inlet nor outlet and are fed by seepage and local runoff. For the most part the plains lakes tend to be of shallow depth and regular shoreline. Pennak (1941) found that 50 plains lakes could be divided into two classes, namely, a non-alkali group containing from 75.68 to 374.00 mg total residue per liter and an alkali group containing from 548.90 to 11,889.70 mg total residue per liter.

There is much intergrading between adjacent zones but on the whole the altitudinal zone scheme has descriptive value. Rawson (1939) has pointed out the modifying influences of morphologic, climatic, and edaphic factors in general lake metabolism. Therefore it does not seem surprising that a certain lake may resemble lakes at a higher or lower elevation more than it does other lakes of the same altitude.

Data and Discussion

Forty-seven species of Entomostraca were identified from ninety-eight Colorado lakes in five altitudinal zones (Table I).

Table I. Number of lakes sampled and number of species occurring per zone

Zone	Lakes	Species
Alpine	5	13
Sub-alpine	49	25
Montane	7	21
Foothills	4	8
Plains	33	31
Total	98	47

Occurrences of Entomostraca relative to altitude appear to divide into three groups and for the sake of convenience will be so considered. The first category contains species occurring both above and below the montane zone, Table II; those found in or above the montane zone, Table III; and lastly those species occurring in or below this zone, Table IV. Three species in the first category, *Cyclops thomasi, Daphnia*[1] *longispina,* and *Daphnia pulex,* occurred in all zones. *Chydorus sphaericus* and *Cyclops vernalis* occurred in all but the foothills zone.

In the lakes sampled *Daphnia longispina* was

[1] After the manuscript had been submitted, the authors became aware of Dr. John L. Brooks' forthcoming revision of the systematics of North American Daphnia. It now appears that more than two species are involved in these collections.

Table II. Occurrence and (in parentheses), percentage of occurrence of Entomostraca in alpine, sub-alpine, montane foothills, and plains lakes in Colorado

Species	Type and Number of Lakes						Altitudinal range, feet (Dodds 1919)
	5 Alpine	49 Subalpine	7 Montane	4 Foothills	33 Plains	98 Total	
Cyclops vernalis	1(20)	4(8.2)	2(28.6)	.....	23(69.9)	30(30.6)	not recorded
C. thomasi	1(20)	27(55)	4(57)	4(100)	12(36.3)	48(48.9)	4,100-11,900
Diaptomus lepotpus	.....	1(2)	.....	1(25)	2(6.1)	4(4.1)	5,300-10,900
D. lintoni	.....	4(8.2)	.....	.....	1(30)	5(5.1)	9,400- 9,600
Chydorus sphaericus	1(20)	20(40.8)	2(28.6)	.....	2(6.1)	25(25.5)	4,100-12,100
Macrothrix hirsuticornis	1(20)	2(4.1)	.....	.....	1(3.0)	4(4.1)	5,300-12,000
Kurycercus lamellatus	1(20)	6(12.2)	.....	.....	1(3.0)	8(8.2)	8,100-12,000
Daphnia longispina	2(40)	34(69.4)	5(71.4)	3(75)	21(63.6)	65(66.3)	5,200-11,300
D. pulex	1(20)	16(32.7)	5(71.4)	1(25)	9(27.3)	32(33)	4,100-11,600
Ceriodaphnia quadrangula	.....	3(6.1)	1(14.3)	.....	12(36.4)	16(16.4)	not recorded
C. reticulata	.....	4(8.2)	2(28.6)	.....	1(3.0)	7(7.1)	4,100-11,100
Scapholeberis mucronata	.....	1(2.0)	1(14.3)	.....	1(3.0)	3(3.0)	4,600- 9,700
Simocephalus vetulus	1(20)	.....	1(14.3)	.....	4(12.2)	6(6.1)	4,100-10,500

the species recorded most often and also the most evenly distributed percentage-wise. It was found in 40% of the alpine lakes, 69.4% of the subalpine, 71.4% of the montane, 75% of the foothills, and 63.6% of the plains lakes. This cladoceran was found in 65 of 98 lakes sampled (66.3%). *C. thomasi,* the species second in number of occurrences (48 times or 49%) was the most widely distributed copepod. Third in number of occurrences (32) was *D. pulex*. *D. pulex* was found more often at the higher elevations than at the low. *C. vernalis* was the second ranking copepod and fourth in total (29) appearances. Unlike *C. thomasi, vernalis* was more common in the plains zone. *Diaptomus lintoni* was recorded by Dodds (1917) in the montane zone (Table II). In the present study *D. lintoni* was recorded from four sub-alpine lakes and one plains lake, Horsetooth Reservior. This lake is an artificial body of water recently created (1949) and directly connected by canals to montane and sub-alpine water sources. *Eurycercus lamellatus* is a cladoceran of wide geographical distribution but was found in only one body of water on the plains, this again was Horsetooth Reservoir. Thomas (1952) found *E. lamellatus* in College Lake, a reservoir filled from Horsetooth. From the above records it would seem that irrigation projects have aided the spread of these two species.

Of the fourteen species recorded in or above the montane zone *Diaptomus coloradensis* and *Polyphemus pediculus* occurred in the alpine and sub-alpine zones as well as the montane, Table III.

TABLE III. Occurrence and percentage of occurrence of Entomostraca in alpine, sub-alpine and montane lakes in Colorado

Species	Type and Number of Lakes				Altitudinal range, feet (Dodds 1917)
	5 Alpine	49 Sub-alpine	7 Montane	61 Total	
Orthocyclops modestus	.....	1(2.0)	.....	1(1.6)	not recorded
Eucyclops agilis	.....	5(10.2)	1(14.3)	6(9.8)	4,100–11,200
Macrocyclops ater	.....	1(2.0)	1(14.3)	2(3.2)	4,400– 4,600
M. albidus	.....	5(10.2)	1(14.3)	6(9.8)	4,100–11,000
Diaptomus arapahoensis	.....	7(14.3)	.....	7(11.5)	10,700–11,200
D. coloradensis	2(40)	33(67.3)	1(14.3)	36(59.0)	7,500–11,300
D. judayi	.....	1(2.0)	.....	1(1.6)	9,100– 9,300
D. shoshone	3(60)	4(8.2)	.....	7(11.5)	9,200–12,200
D. connexus	1(20)	.....	.....	1(1.6)	not recorded
Alona affinis	.....	1(2.0)	.....	1(1.6)	8,100–11,100
Acroperus harpae	.....	1(2.0)	.....	1(1.6)	8,100–10,900
Macrothrix montana	.....	1(2.0)	.....	1(1.6)	10,800–11,100
Polyphemus pediculus	1(20)	8(16.4)	1(14.3)	10(16.4)	not recorded
Holopedium gibberum	1(20)	3(6.1)	.....	4(6.6)	9,500–11,000

Diaptomus connexus was the sole species found only in the alpine zone. *Diaptomus shoshone* and *Holopedium gibberum* were found only in the alpine and subalpine zones. Six species, *Orthocyclops modestus, Diaptomus arapahoensis, Diaptomus judayi, Alona affinis, Acroperus harpae,* and *Macrothrix montana* were recorded only in sub-alpine lakes. *Eucyclops agilis, Macrocyclops ater,* and *M. albidus* occurred in the sub-alpine and montane zones.

Nineteen species were found in and below the montane zone. Three, *Diaptomus nudus, Diaptomus oregonensis* and *Bosmina longirostris* were found in the montane, foothills and plains lakes, Table IV. Twelve species were recorded only from the plains lakes. *Diaptomus oregonensis* has not been previously recorded from Colorado, however this diaptomid is distributed transcontinentally in the northern states and Canada. Of the seven lakes in which *D. oregonensis* was found, Parvin Lake at 8,200 feet is the highest. The other six are more or less directly connected by streams or canals to Parvin.

The occurrence of *D. oregonensis* in this group of lakes is of considerable ecological interest. Marsh (1918) said that *D. oregonensis* was an example of a species apparently equally well adapted to deep or shallow water. Pennak (1953) states that *D. oregonensis* is one of a group of cold-water forms "occurring only in the northern states and in deep lakes." One pond in which

TABLE IV. Occurrence and percentage of occurrence of Entomostraca in montane, foothills, and plains lakes in Colorado

Species	Type and Number of Lakes				Altitudinal range, feet (Dodds 1917)
	7 Montane	4 Foothills	33 Plains	44 Total	
Diaptomus clavipes	1(14.3)	.....	5(15.2)	6(13.6)	4,100– 5,500
D. nudus	3(42.8)	2(50.0)	5(15.2)	10(22.7)	5,200–11,000
D. oregonensis	1(14.3)	1(25.0)	5(15.2)	7(15.9)	not recorded
D. siciloides	.....	.....	20(60.6)	20(45.4)	4,100– 5,000
Alona costata	.....	.....	1(3.0)	1(2.3)	not recorded
A. guttata	.....	.....	4(12.2)	4(9.1)	4,200– 9,300
A. quadrangularis	.....	1(25.0)	.....	1(2.3)	not recorded
A. rectangula	.....	.....	3(9.1)	3(6.9)	5,200–11,200
Pleuroxus aduncus	.....	.....	1(3.0)	1(2.3)	5,100– 5,400
P. denticulatus	.....	.....	1(3.0)	1(2.3)	5,100– 5,400
Dunhevedia crassa	.....	.....	1(3.0)	1(2.3)	5,200– 8,800
Macrothrix laticornis	.....	.....	2(6.1)	2(4.6)	not recorded
Daphnia magna	.....	.....	1(3.0)	1(2.3)	not recorded
Ceriodaphnia pulchella	.....	.....	1(3.0)	1(2.3)	9,100– 9,200
Moina brachiata	.....	.....	1(3.0)	1(2.3)	4,100– 4,500
M. macrocopa	.....	.....	2(6.1)	2(4.6)	not recorded
Diaphanosoma brachyurum	2(28.6)	.....	5(15.2)	7(15.9)	not recorded
Leptodora kindti	1(14.3)	.....	2(6.1)	3(6.9)	not recorded
Bosmina longirostris	6(85.7)	4(100)	19(57.6)	29(65.9)	4,000– 5,300

oregonensis was collected occupied what appeared to be a disused gravel pit. It is a fraction of an acre in surface and is quite shallow. Apparently the water level is maintained by seepage with perhaps occasional influxes of irrigation water.

The presence of *Leptodora kindti* in Colorado was first recorded by Olive in 1953 from Parvin Lake. During collection of material for this paper *L. kindti* was taken from two irrigation reservoirs near Fort Collins. Both of these reservoirs also contained *D. oregonensis*. *L. kindti* is widely distributed in the northern states in the Great Lakes area. As pointed out by Olive (1953b) this disjunction in distribution is best explained as a chance introduction by fishermen. It would be easy for ephippial eggs to reach the plains reservoirs through the streams and canals. But Reservoir No. 2 in which considerable numbers of *L. kindti* were taken is a warm, shallow, turbid body of water—in short quite different from lakes in which *L. kindti* usually appears. The specimens taken included both adult and immature individuals, indicating a reproducing population.

Dodds in 1915 predicted that *Bosmina longirostris* would be found in the mountains. In 1924 in reporting on the Shantz collections from the Pikes Peak region Dodds listed *B. longirostris* from one lake near 11,00 feet. Pennak (1950) recorded *B. longirostris* in Hotel Twin Lake on Grand Mesa (sub-alpine). However it appears that *Bosmina* is more commonly found at lower elevations.

One cladoceran, *Leydigia quadrangularis*, was recorded from Skaguay Reservoir, the sole species found only in the montane zone.

In the following account italicized numbers refer to specific lakes in Table V. To save space records of the most commonly occurring species have been omitted.

CLADOCERA

Latona setifera (O.F.M.)
Records: Dodds (1908, 1924).

Holopedium gibberum Zaddock
Collected: Alpine *98;* sub-alpine *51, 79, 101.*
Recorded: Dodds (1915), Pennak (1944) *87.*

Diaphanosoma brachyurum (Lieven)
Collected: Montane *38, 88;* Plains *3, 75, 78. 17.*
Records: Dodds (1924), Pennak (1955a).

Diaphanosoma leuchtenbergianum Fischer
Records: Pennak (1944) *6, 19, 9.*

Daphnia longispina (O.F.M.)
Collected from 65 lakes in all zones.

Daphnia magna Straus
Collected: Plains *31.*

Daphnia pulex (de Geer)
Collected from 32 lakes in all zones.

Scapholeberis mucronata (O.F.M.)
Collected: sub-alpine *99;* montane *96;* plains *84.*
Recorded: Beardsley (1902), Dodds (1915), Thomas (1952) *25.*

Simocephalus serrulatus (Koch)
Records: Dodds (1915).

Simocephalus vetulus (O.F.M.)
Collected: alpine *52;* montane *96;* plains *31, 7, 58, 74.*
Recorded: Beardsley (1902), Dodds (1908, 1924).

Ceriodaphnia pulchella Sars
Collected: plains *61.*
Recorded: Dodds (1915), Pennak (1949) *6, 9, 19, 32;* Thomas (1952) *25.*

Ceriodaphnia quadrangula (O.F.M.)
Collected from 16 sub-alpine, montane and plains lakes.

Ceriodaphnia reticulata (Jurine)
Collected: sub-alpine *13, 27, 29, 47;* montane *13, 96;* plains *7.*
Recorded: Dodds (1924), Thomas (1952), Pennak (1955a).

Moina affinis Birge
Records: Beardsley (1902), Dodds (1915).

Moina brachiata (Jurine)
Collected: plains *41.*
Records: Dodds (1915).

Moina macrocopa Straus
Collected: plains *16, 94.*
Records: Birge (1917).

Bosmina longirostris (O.F.M.)
Collected from several plains, foothills and montane lakes.
Records: Dodds (1924), Pennak (1950, 1955a, 1955b).

Drepanothrix dentata (Euren)
Record: Dodds (1915).

Streblocerus serricaudata (Fischer)
Record: Dodds (1915).

Macrothrix hirsuticornis Norman and Brady
Collected: alpine *52;* sub-alpine *102, 79;* plains *7.*
Recorded: Dodds (1915).

Macrothrix laticornis (Jurine)
Collected: plains *16, 86.*
Recorded: Dodds (1908).

Macrothrix montana Birge
Collected: sub-alpine *33.*
Recorded: Dodds (1915).

Eurycercus lamellatus (O.F.M.)
Collected: alpine 98; sub-alpine *66, 79, 100, 13, 102;* plains *25, 42.*
Recorded: Dodds (1915).
Camptocercus rectirostris Schoedler
Recorded: Dodds (1915).
Acroperus harpae Baird
Collected: sub-alpine *93.*
Recorded: Dodds (1915).
Kurzia latissima (Kurz)
Recorded: Beardsley (1902), Dodds (1915).
Graptoleberis testudinaria (Fischer)
Recorded: Dodds (1915).
Leydigia quadrangularis (Leydig).
Collected: montane *88.*
Recorded: Dodds (1915).
Alona affinis (Leydig)
Collected: sub-alpine *79, 101.*
Recorded: Dodds (1908).
Alona costata Sars
Collected: plains *42.*
Apparently not recorded from Colorado previously.
Alona guttata Sars
Collected: plains *78, 42, 83, 31.*
Recorded: Dodds (1915).
Alona glacialis Birge
Recorded: Beardsley (1902); Dodds (1908).
Probably synonymous with *A. guttata* (Dodds, 1915).
Alona quadrangularis (O.F.M.)
Collected: foothills *28.*
Recorded: Dodds (1908).
Alona rectangula Sars
Collected: plains *31, 58, 7.*
Recorded: Dodds (1915), Thomas (1952).
Dunhevedia crassa King
Collected: plains *61.*
Recorded: Dodds (1915).
Pleuroxus aduncus (Jurine)
Collected: plains *61.*
Recorded: Dodds (1915).
Pleuroxus denticulatus Birge
Collected: plains *86.*
Recorded: Dodds (1915), Thomas (1952).
Pleuroxus procurvatus Birge
Recorded: Dodds (1915).
Alonella excisa (Fischer)
Recorded: Dodds (1915).
Alonella exigua (Lilljeborg)
Recorded: Dodds (1915).
Chydorus sphaericus (O.F.M.)
Collected in 25 lakes in all zones.
Polyphemus pediculus (Linne)
Collected from 10 montane and sub-alpine lakes.
Apparently not hiterto recorded in Colorado.
Leptodora kindti (Focke)
Collected: montane *65;* plains *78.*
Recorded: Olive (1953b).

COPEPODA

Diaptomus albuquerquensis Herrick
Recorded: Dodds (1908), Marsh (1929).
Diaptomus arapahoensis Dodds
Collected: sub-alpine *15, 68, 69, 70, 71, 54, 101.*
Recorded. Dodds (1916), Wilson (1953).
Diaptomus clavipes Schacht
Collected: montane *65;* plains *42, 90, 95, 31, 106.*
Recorded: Beardsley (1902), Dodds (1908), Marsh (1929).
Diaptomus coloradensis Marsh
Collected from 36 lakes and reservoirs between 9,700 and 11,000 feet elevation.
Recorded: Dodds (1915), Marsh (1918).
Diaptomus connexus Light
One individual, tentatively identified by Mrs. Mildred S. Wilson as belonging to this species, was collected from Naylor Lake (alpine).
Recorded: Wilson (1954).
Diaptomus judayi Marsh
Collected: sub-alpine *99.*
Recorded. Marsh (1929).
Diaptomus leptopus Forbes
Collected: sub-alpine *37;* foothills *28;* plains *42, 78.*
Recorded: Dodds (1915), Marsh (1929), Pennak (1955a). Some older records as *D. piscinae.*
Diaptomus lintoni Forbes
Collected: sub-alpine *27, 29, 50, 51;* plains *42.*
Recorded: Dodds (1915); Marsh (1929).
Diaptomus nudus Marsh
Collected: montane *65, 85, 88;* foothills, *28, 56;* plains *42, 78, 86, 81.*
Recorded: Dodds (1915), Marsh (1929).
Diaptomus oregonensis Lilljeborg
Collected: montane *65;* foothills *80;* plains *73, 61, 78, 83, 94.*
Apparently not recorded before from Colorado.
Diaptomus pallidus Herrick
Recorded: Dodds (1915).
Diaptomus shoshone Forbes
Collected: alpine *91, 98; sub-alpine 26, 50, 68, 71, 107.*
Recorded: Marsh (1929), Pennak (1944, 1955b).

TABLE V. Location of Colorado lakes by county and drainage

Lake	Zone	County	Drainage	
1. Angel L.	P	Weld	Platte	†
2. Alexander L.	S	Delta	Colo.	†
3. Allen's L.	P	Boulder	Platte	†, ‡
4. Barker R.	F	"	"	†
5. Barron L.	S	Delta	Colo.	†, ‡
6. Baseline R.	P	Boulder	Platte	†
7. Batman R.	P	Weld	"	†
8. Bear L.	M	Larimer	"	‡
9. Beasley R.	P	Boulder	"	‡
10. Beaver L.	S	Delta	Colo.	†
11. Big Butts L.	S	"	"	†
12. Big Creek L.	S	"	"	†
13. Big Eggleston L.	S	"	"	†, ‡
14. Big Lake				‡
15. Big McIntyre L.	S	Larimer	Platte	†
16. Boettcher R.	P	"	"	†
17. Boettcher, E. basin	P	"	"	†
18. Bonham R.	S	Delta	Colo.	†
19. Boulder R.	P	Boulder	Platte	‡
20. Butts L.	S	Delta	Colo.	†
21. Carbody L.	P	Weld	Platte	†
22. Clear Creek R.	S	Lake	Ark.	†
23. Clear L.	M	Clear Creek	Platte	†
24. Clover Basin R.	P	Boulder	Platte	†
25. College L.	P	Larimer	"	‡
26. East Rainbow L.	S	"	"	†
27. Elmo L.	S	"	"	†
28. Estes L.	F	"	"	†
29. Fishook L.	S	Routte	Colo.	†
30. Forest L.	S	Delta	"	†
31. Fossil Creek R.	P	Larimer	Platte	†
32. Gaynor R.	P	Boulder	"	‡
33. Glacier Spring L.	S	Delta	Colo.	†
34. Grand L.	M	Grand	Colo. & Platte*	†, ‡
35. Granby No. 1 R.	S	Delta	Colo.	†
36. " No. 5 R.	S	"	"	†
37. " No. 11 R.	S	"	"	†
38. Granby R.	M	Grand	Colo. & Platte*	†
39. Green L.	S	Douglas	Platte	†
40. Hayden's R.	P	Boulder	"	‡
41. Hillsborough R.	P	Weld	"	†
42. Horsetooth R.	P	Larimer	"	†
43. Hotel Twin L.	S	Delta	Colo.	†, ‡
44. Island L.	S	"	"	†
45. Jefferson L.	S	Park	Platte	†
46. Jumbo R.	P	Logan & Sedgewick	"	†
47. Kiser Slough L.	S	Mesa	Colo.	†
48. Kossler L.	F	Boulder	Platte	‡
49. Little Gem L.	S	Mesa	Colo.	†
50. Little Lost L.	S	Jackson	Platte	†
51. Lost L.	S	"	"	†
52. Loveland Pass L.	A	Summit	Colo.	†
53. Loveland R.	P	Larimer	Platte	†
54. Lower Camp L.	S	"	"	†
55. Lower Sandbar L.	S	"	"	†
56. Mary's L.	F	"	"	†
57. Matarch L.	S	Delta	Colo.	†
58. McFarland R.	P		Platte	†
59. Mesa L.	S	Mesa	Colo.	†
60. Naylor L.	A	Douglas	Platte	†
61. Neff L.	P	Weld	Platte	†
62. New Windsor R. upper basin	P	"	"	†
63. New Windsor R. lower basin	P	"	"	†
64. North Sterling R.	P	Logan	"	†
65. Parvin L.	M	Larimer	"	†
66. Percy L.	S	Jackson		†
67. Pond	P	Larimer	Platte	†

TABLE V (continued)

Lake	Zone	County	Drainage	
68. Rawah No. 1 L.	S	"	"	†
69. " No. 2 L.	S	"	"	†
70. " No. 3 L.	S	"	"	†
71. " No. 4 L.	A	"	"	†
72. Reed L.	S	Delta	Colo.	†
73. Res. No. 2	P	Larimer	Platte	†
74. Res. No. 3- N. Poudre	P	"	"	†
75. Res. No. 4-N. Poudre	P	"	"	†
76. Rimrock L.	S	Delta	Colo.	†
77. Rockland L.	S	"	"	†
78. Rocky Ridge R.	P	Larimer	Platte	†
79. Round L.	S	Routte	Colo.	†
80. Seamen R.	F	Larimer	Platte	†
81. Seeley L.	P	Weld	"	†, ‡
82. Sterling R.	P	Logan	"	†
83. Setzer's R.	P	Larimer	"	†
84. Severance Rd. R.	P	Weld	"	†
85. Shadow Mtn. R.	M	Grand	Colo. & Platte	†
86. Sheldon L.	P	Larimer	Platte	†
87. Silver L.	M			‡
88. Skaguay R.	M	Teller	Ark.	†
89. Skookum L.	S	Delta	Colo.	†
90. Sterkel's R.	P	Larimer	Platte	†
91. Sugar Bowl L.	A	"	"	†
92. Summit L.	A			‡
93. Teal L.	S	Jackson	Platte	†
94. Temp Pond	P	Larimer		†
95. Timnath R.	P	"	Platte	†
96. Tolland (Ponds)	M	Gilpin	Platte	†, ‡
97. Trickle Park L.	S	Delta	Colo.	†
98. Turquoise L.	A	Lake	Ark.	†
99. Twin L.	S	"	"	†
100. Twin L.	S	Larimer	Platte	†
101. Upper Sandbar L.	S	"	"	†
102. Vela R.	S	Delta	Colo.	†
103. Ward L.	S	"	"	†, ‡
104. West Rainbow L.	S	Larimer	Platte	†
105. Williams L.	P	"	"	†
106. Windsor R.	P	Weld	"	†
107. Young's Creek R.	S	Delta	Colo.	†
108. " " R. No. 2	S	"	"	†

A—alpine
M—montane
P—plains
S—sub-alpine
F—foothills
Platte—Platte River drainage
Colo.—Colorado River drainage
Ark.— Arkansas River drainage
*Connected by Colorado-Big Thompson Project tunnel.
†Collection examined by authors.
‡Literature records.

Diaptomus sicilis Forbes
Recorded: Beardsley (1902).

Diaptomus siciloides Lilljeborg
Collected from 20 plains lakes.
Recorded: Dodds (1908), Marsh (1929), Pennak (1949) *3, 6, 9, 19, 40, 32, 48.*

Diaptomus signicauda Lilljeborg
Recorded: Dodds (1915).

Diaptomus tyrrelli Poppe
Recorded: Pennak (1950).

Diaptomus novamexicanus Herrick
Recorded: Dodds (1924). As *D. washingtonensis*

Cyclops thomasi Forbes
Collected from 48 lakes at all altitudes.
Former records as *C. bicuspidatus.*
Cyclops vernalis
Collected from 30 lakes in all zones but foothills.
Paracyclops fimbriatus (Fischer)
Recorded: Neldner and Pennak (1955) from alpine pond.
Eucyclops agilis (Koch)
Collected: sub-alpine *50, 66, 13, 77, 35;* montane *96.*
Recorded: Dodds (1915) as *Cyclops serrulatus,* Pennak (1955b).
Macrocyclops ater (Herrick)
Collected: sub-alpine *100;* montane *96.*
Recorded: Beardsley (1902) as *Cyclops ater.*
Macrocyclops albidus (Jurine)
Collected: sub-alpine *11, 102, 47, 29, 35;* montane *96.*
Recorded: Dodds (1915) as *Cyclops albidus,* Pennak (1955b).
Orthocyclops modestus (Herrick)
Collected: sub-alpine *51.*

When the foregoing records are examined it becomes evident that certain entomostracans have much wider altitudinal ranges than others. Many of the cladocerans and some cyclopoids are bottom dwellers or are closely associated with aquatic vegetation and hence are usually not taken by ordinary plankton collecting methods. Taxonomic uncertainties further obscure the picture, but even if the infrequently collected species are disregarded there still remains a group of animals common to all zones and another group of species exhibiting restricted altitudinal range (Fig. 1).

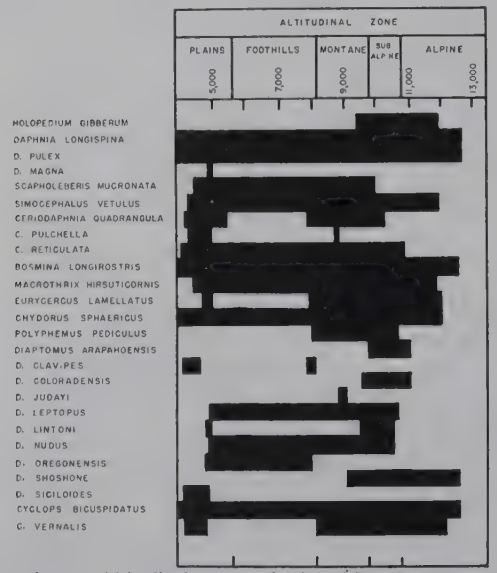

FIG. 1. Altitudinal ranges of selected Entomostraca in Colorado.

Cladocerans of the former group such as *Daphnia longispina, Daphnia pulex, Ceriodaphnia reticulata, Bosmina longirostris, Macrothrix hirsuticornis, Eurycercus lamellatus,* and *Chydorus sphaericus* appear with regularity on lists of plankton organisms from Europe and North America, indeed *C. sphaericus* and *D. pulex* are essentially cosmopolitan (Pennak 1953).

Holopedium gibberum and *Polyphemus pediculus* are often considered as boreal species that occur at high altitudes in the southern parts of their ranges, however Coker (1954) recorded *Polyphemus* in North Carolina and pointed out that this species may have a wider range than formerly assumed.

The discontinuous altitudinal distribution of *Ceriodaphnia quadrangula, C. pulchella, Eurycercus lamellatus, Diaptomus clavipes,* and *Cyclops vernalis* is probably an artifact of collection or perhaps due to the small number of foothills lakes sampled. The occurrence of *Diaptomus lintoni* in one plains reservoir has been commented on above. *Daphnia magna* was collected in the vegetation of the littoral area in Fossil Creek Reservoir. This cladoceran is apparently of wide distribution but, perhaps owing to the weedy habitats in which it lives, is seldom collected.

If the cyclopoid species are as widely distributed as the literature would indicate, then there is nothing worthy of comment on the occurrence in Colorado of the species listed here. Coker (1943) referred to *Mesocyclops edax* as "probably our most common limnetic cyclopoid" and Pennak (1953) says "widely distributed" of *Orthocyclops modestus.* Yet there is no record for Colorado of the former, and this paper appears to include the first for *O. modestus. Paracyclops fimbriatus* likewise is reputed to be of wide occurrence, yet the record by Neldner and Pennak (1955) appears to be the only one for this species from Colorado. Yeatman (1944) has pointed out that *Cyclops vernalis* is extremely common but very often misidentified because of errors that became incorporated into the early literature on copepods in North America. When it is considered that the cyclopoid fauna of Colorado is at least as well known as that of other western States, there appears to be need of more detailed records upon which to base an evaluation of the distribution of this copepod group.

A different situation exists in the calanoid copepods where distribution is better known. Wilson (1953, 1953b) has indicated that definite patterns of distribution may exist in the calanoid copepods of North America. Of the eleven species of *Diaptomus* collected during this survey, five exhibit a high altitude distribution both within Colorado and outside of the state. *D. coloradensis, D. arapahoensis,* and *D. judayi* were collected in the sub-alpine zone; *D. shoshone* occurred in both sub-alpine and alpine zones. *D. coloradensis* is known from the Rocky Mountains in Colorado and Utah; *D. arapahoensis* and *D. judayi* have been found only in the Rockies; *D. shoshone* is known only from high altitudes in the Rockies and in the Sierra Nevada Mountains of California (Wilson, *in press*). *D. lintoni* is also a Rocky Mountain species and appears in Colorado to be most frequently found at the higher elevations.

D. clavipes was collected in the plains and montane zones. *D. clavipes* occurs in the Rocky Mountains at lower elevations throughout the United States and into northern Mexico, adjacent southwestern states and east to the Mississippi River (Wilson 1955)—a pattern of low altitude Rocky Mountain—Southern Great Plains distribution.

In contrast, *D. nudus,* collected in the montane, foothills and plains zones, shows still another pattern of distribution. *D. nudus* occurs in the Rocky Mountains, Alberta, Saskatchewan, Manitoba, and Alaska (Wilson, personal communication) and in British Columbia (Carl 1940)—thus exhibiting a pattern of Rocky Mountain, western and Northern Great Plains distribution.

What is the effect of altitude upon the distribution of Entomostraca in Colorado? One of the outstanding differences between altitudinal zones is in the climatic conditions, particularly in air temperature and in precipitation. The effects of these two agents on limnological conditions are indeed far-reaching; singly and in combination they affect such factors of the aquatic environment as water temperature, rate of chemical solution of substrate, rate of decay of organic matter, rate of deposition, flushing, and turbidity. Marsh (1929) stated "without doubt the principal controlling factor in distribution is temperature." Carl (1940) concluded that the pattern of distribution of Entomostraca in British Columbia was the result of many factors, but the temperature effect was of prime importance.

There are, however, important differences between lakes of the various zones which are not directly related to altitude. Such factors as basin morphology and composition of the substrate and watershed are independent of altitude. Rawson (1942) demonstrated the effect and interplay of climatic, edaphic and morphometric conditions in some Canadian alpine lakes. The alpine lakes of the present study are probably a more homogenous group than are the lakes of the other zones. The comparatively large number of species found within the sub-alpine, montane and plains zones is most certainly a reflection of the wider range of habitats occurring in these zones.

Thus altitudinal distribution of Entomostraca in this region probably depends for the most part on habitat availability within the various zones; the greater the number of habitats, the more species found. The habitats are the results of the interaction of climatic, edaphic, and morphometric factors. The effect of altitude is probably expressed through meteorological conditions, particularly temperature and precipitation, obtaining in the various zones.

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Summary

1. Ninety-eight Colorado lakes were sampled to determine the altitudinal distribution of some Entomostraca in Colorado.

2. The lakes of Colorado are classified in altitudinal zones as plains, foothills, montane, sub-alpine or alpine.

3. Four species of copepods and nine species of cladocerans occurred both above and below the montane zone.

4. Nine species of copepods and five species of cladocerans occurred in or above the montane zone. Four species of copepods and fifteen species of cladocerans occurred in or below the montane zone.

5. Seventeen species of Copepoda were collected, five other species are recorded in the literature; thus twenty-two species are known to occur in Colorado.

6. Thirty species of Cladocera were collected, fourteen other species are recorded from the literature for a total of forty-four species from the state.

7. As far as could be determined *Alona costata, Polyphemus pediculus, Diaptomus oregonensis,* and *Orthocyclops modestus* have not been previously recorded in Colorado.

8. Interaction of climatic, morphometric and edaphic factors in relation to altitudinal zones and entomostracan distribution are discussed.

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VITAL LIMITS AND RATES OF DESICCATION IN SALAMANDERS[1]

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Adaptations of major importance in the evolution of life on dry land are those increasing the resistance of an organism to desiccation. Among vertebrates, modern amphibians represent a transitional stage since, in addition to truly amphibious members, the group contains both completely aquatic and completely terrestrial forms; yet, when exposed to air, all lose water through the skin. Some amphibians live in surprisingly dry habitats, but all must have access to water other than that obtained in food. Two special adaptations of amphibians to desiccation are apparent: (1) the ability of some amphibians to endure large losses of body water. Thorson and Svihla (1943) and Littleford *et al.* (1947) subjected various amphibians to desiccation under controlled conditions and found that the ability to endure loss of body water is in most instances correlated with the dryness of their habitats; (2) another adaptation may be the comparatively slow rate at which some amphibians lose body water—or the fast rate at which they regain it (Thorson and Svihla 1943; Littleford *et al.* 1947; Cohen 1952; Thorson 1955, 1956).

The present paper supplements the work of these authors and discusses some modification of the methods over those used in previous studies of this type. The amphibians studied were salamanders of the following species: *Batrachoseps attenuatus* (7 individuals), *Ensatina eschscholtzi xanthoptica* (6), *Aneides lugubris* (5), *A. Ferreus* (3), *A. flavipunctatus niger* (6), *Plethodon elongatus* (2), *P. dunni* (1), and *Rhyacotriton olympicus variegatus* (5). Localities from which the study animals were obtained are indicated in figure 4.

APPARATUS

The dessication apparatus was a modification of that first used by Hall (1922).[2] Air from the laboratory compressed-air supply was passed through two jars that acted as traps to prevent backflow of acid into the air supply line and which served as pressure buffers to stabilize variations in air flow. An adjustable clamp between the jars regulated the rate of flow. Four bottles with concentrated sulfuric acid dried the air to a relative humidity of roughly 2%.[3] Acid tended to discolor with time, but maintained a high concentration for many hours. The specific gravity was taken frequently to assure that it stayed at 1.8. A bottle containing NaOH pellets removed acid fumes from the dry air and a trap separated the acid from the hydroxide. This was installed to prevent a mixture of acid and hydroxide which might result from sudden pressure changes. A bottle filled with glass wool removed physical impurities from the air. A tap off the main air line led air into a beaker of water containing a few drops of hematoxylin. The presence of acid turns hematoxylin from red to yellow. Since this did not occur, acid fumes were considered to be eliminated. A U-tube manometer was calibrated to read in cubic centimeters of air flow per minute. Another control clamp was attached to the manometer inlet.

The dehydration chamber (Fig. 1A) consisted of a glass tube approximately 2½ inches in diameter and one foot in length, tapered at the outlet. The stopper was provided with three holes for thermometer, air inlet, and manipulator (by means of which the animals being tested could be handled during dehydration). The chamber contained a copper screen floor on which the animals could rest without coming into contact with the glass sides of the chamber. If salamanders rest on glass they tend to adhere as they become dehydrated and, in consequence, struggle more than they would if their movements were less impeded. This may seriously weaken them. The screening has the further advantage of allowing maximum exposure of the surface of the animal to air. Evaporation rate would vary with the degree of "hugging" of a solid substrate by the salamander.

A museum-jar desiccation chamber (Fig. 1B) described by Hall (1922) and also used, with various modifications, by Thorson and Svihla (1943), Thorson (1955, 1956), Littleford *et al.* (1947), and Cohen (1952),[4] was first used here,

[1] I wish to thank Robert C. Stebbins of the University of California for his aid and advice during the course of the work and Frank A. Pitelka and Sherburne F. Cook of the same University for reading the paper in manuscript. I am also indebted to Thomas Thorson, Robert A. Littleford and Nathan Cohen for their helpful comments.

[2] The apparatus is figured in Hall's paper and is therefore not illustrated here.

[3] Relative humidity was determined by potassium pentoxide absorption of water.

[4] Cohen actually used a Scheibler desiccator, but this chamber is as subject to turbulence as a museum jar because the shape is the same.

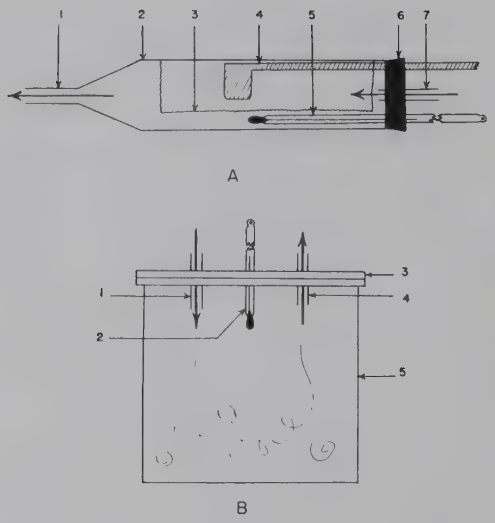

FIG. 1. A. Desiccation chamber of tubular design used in the experiments. (1) outlet, (2) glass tube 1 foot long, (3) wire screen floor, (4) manipulator, (5) thermometer, (6) stopper, (7) inlet.

B. Museum-jar type of desiccation chamber in which considerable turbulence occurs (see text). (1) inlet, (2) thermometer, (3) clamp-on lid, (4) outlet, (5) chamber.

but it was thought that this type of chamber might lead to excessive turbulence of the circulating air; that is, air having once passed over an animal and having had its relative humidity raised by the water given off by the animal, could come into contact with the animal again. Adolph (1932) has shown that frogs lose water at a rate which varies inversely with relative humidity. Therefore, if the relative humidity in the chamber varies or is elevated, the rate of desiccation will vary accordingly. In several preliminary experiments using the museum-jar type of desiccation chamber, I was able to show that *Batrachoseps attenuatus* took up to one-third again as long to reach the lethal point in the jar-shaped as in the tube-shaped chamber even though the air flow through both was the same. (A simple calculation involving the weight of water given off by the animal in a given time and the volume of the chamber showed that the relative humidity in the museum jar I used in the preliminary experiments might have risen as high as 20%.)

The turbulence effect which raises the relative humidity in the museum-jar type of chamber and which is minimized in the tube-shaped type of chamber (because of direct flow of air over the animal from inlet to outlet) does not apparently influence the amount of water lost before the lethal point providing that air flow is held at a reasonably slow rate. Experiments on rates of desiccation in which the jar-shaped chamber has been used should be reexamined to determine just what the relative humidity in the chamber might have been during the entire course of the experiment.

Physical factors influencing the evaporation rate were controlled in the experiments. The apparatus was maintained at 22° ± 1° C. Shelford (1913) states that a rise in temperature of 15° to 17° C will double the rate of evaporation of water through the skin. Although 22° C is somewhat higher than the salamanders commonly experience in the field, laboratory animals have shown no ill effects from exposure to such temperatures. The air pressure in the system was maintained at a constant level and was that of one atmosphere. By means of the control clamps, air flow rate was maintained at 2000 cc/min. High rates are much more injurious than low ones, but it appears that this rate was not so high as to result in death from causes other than loss of body water. That this is so is indicated by comparison of my results with those of Stebbins (1954). He exposed *Ensatina* to ordinary atmosphere. Temperature, humidity, air pressure, and light were essentially constant throughout his experiment. Although his animals took from 2 hr 13 min to nearly 11 hr to reach the leathal point (differences due to the sizes and relative surface areas of the animals), the percentage of the total weight lost at that point coincides closely with my results. The percentage weight loss at the lethal point, an average of four individuals, was about 41% as compared with my figure of 39.2%.

PROCEDURE

As far as possible, homogeneous samples of each species were obtained. An effort was made to collect individuals of a given species from the same general locality and at the same time of year. In some instances, however, this could not be accomplished.

After collection, the animals were washed and stored in clean glass jars containing a paper towel saturated with water. Storage was at 13° C, a temperature at which all the species of salamanders studied may be kept alive and in good condition for several months without feeding. The majority of the animals was stored 3 days to 2 weeks, but a few were stored a month. At the time of desiccation, all were probably post-absorptive since all had ceased to defecate and none was fed in captivity. The post-absorptive state was desired because differences in the weight and nature of food in the guts of different individuals could influence the results.

The desiccation procedure followed. Animals were washed, dried with a paper towel, weighed, desiccated to the Critical Activity Point (CAP, see below), weighed, desicated to the Lethal Point (LP, see below), weighed again, and returned to the jars containing wet paper. Weighing both at the CAP and LP necessitated removing the animals from the chamber and took no longer than one minute (usually less). The time of weighing was included in the calculation of the length of the desiccation period. The weighing period was so short in relation to the total desiccation time that no significant error is introduced by this method.

Difficulty was encountered in the determination of the lethal point. A characteristic which might be easily detected, which occurs suddenly, and which is constant for all species tested was desired. It was hoped that something more critical than a dry, shrivelled appearance, darkened skin and lack of activity (used by Thorson and Svihla 1943) and cessation of throat movements (used by Littleford *et al.*, 1947) could be found. The latter criterion is not an accurate indication of the lethal point because of both intraspecific and interpecific variability. For example, I observed that both *Rhyacotriton* and *Batrachoseps* halted throat movements at almost any time, whereas *Aneides* and *Ensatina* had more regular throat movements that persisted to near the lethal point. Another criterion that might have been used was the cessation of the flow of blood in the capillaries of the skin, but this was observable in only a few of the more lightly pigmented animals under the conditions of these experiments.

The criterion finally used was the loss of the righting reaction which occurred as follows: near the lethal point the animal gradually lost its ability to crawl. Paralysis, particularly of the hindquarters, was generally observed, but the animal retained its ability to right itself until, quite close to the lethal point and quite suddenly, the animal lost this ability. When one becomes familiar with this chain of events, the time of the loss of the righting reaction may be pin-pointed with a good degree of objectivity, in contrast to the other criteria mentioned. The manipulator in the chamber is used to turn the animal gently on its back. This handling apparently has no ill effects.

In these experiments, two points were checked as follows: (1) Critical Activity Point (CAP). This is the point, close to the true lethal point, marked by the loss of the righting reaction. It is the point used for comparative purposes. (2) The Lethal Point (LP). This point occurred closely following the CAP and was often accompanied by convulsive writhing. In the absence of writhing, Thornson's criteria, mentioned above, were used. That one can err in these subjective determinations of the lethal point is illustrated by Table I. All *Aneides lugubris*, for instance, lived through the desiccation procedure and all *A. flavipunctatus* were killed. Both of these species appeared to be dead, as indicated by Thorson's criteria, but both showed a clear-cut loss of righting reaction.

After one or two days, the salamanders were removed from their containers once more, checked for evidences of life, weighed to determine how much water had been regained, sexed, measured, and placed over $CaCl_2$ for dehydration to dry weight. (The dry weight over $CaCl_2$ is not the absolute dry weight since slightly more water could have been extracted in an oven. It is, however, adequate for comparative purposes).

Results

The results of the desiccation experiments are shown in Table I and Figure 3. The CAP and LP are expressed in two ways. First, the weight losses at the CAP and LP are calculated as percentages of the starting weight. Second, the percentage of the body as dry weight is calculated as the percentage of the body weight represented by dry matter at the CAP and LP. These two methods of representation give slightly different tolerance pictures (see Table I and discussion below) since the percentage of the body as dry weight at the CAP and LP does not take the starting weight—therefore the total body water—into account while the percentage of weight loss

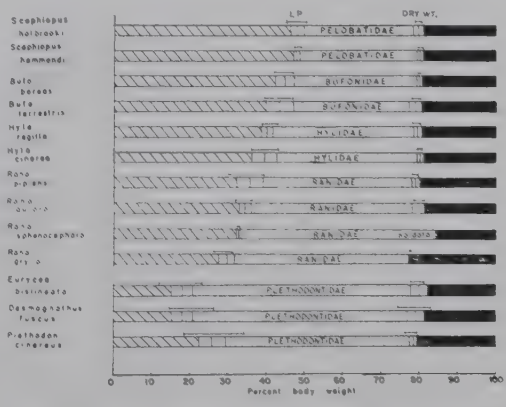

FIG. 2. Diagrammatic representation of the percentages of dry weight (black), of water that may be lost before the lethal point is reached (cross-hatched), and of water remaining in the body at the lethal point (stippled). Data for the ten species of frogs are taken from Thorson and Svihla (1943) and those for the three species of salamanders are after Littleford *et al.* (1947). The ranges of variation are given by the horizontal lines above the bar diagrams. Left blank on the bars are spaces corresponding to $\pm$ 2 $\times$ the Standard Error of the Mean.

TABLE I. Results of the desiccation experiments with salamanders. See text for explanation of Critical Activity Point, Lethal Point, percentage of weight loss, and the percentage of the body as dry weight; (a) individuals dehydrated in the museum jar type of chamber; (b) females containing ova

Species	Number of Individual	Sex	Starting weight, g	Critical Activity Point (CAP)			Lethal Point (LP)			Death	Dry weight, g
				% weight loss as water	% body as dry weight	Time in minutes	% weight loss as water	% body as dry weight	Time in minutes		
Batrachoseps attenuatus	22	..	1.615	24.3	35.6	45	28.7	37.8	59	no	0.435
	23	..	1.612	31.4	37.4	96	35.1	39.5	85	yes	0.414
	35	..	1.321	26.5	....	53	29.1	....	60	....	.....
	36	..	1.422	29.3	....	64	32.7	....	72	....	.....
	39	♂	1.294	26.9	38.2	54	28.5	39.0	59	yes	0.361
	40	♀	1.206	31.1	35.9	56	33.6	37.2	62	no	0.298
	42	..	1.367	33.1	42.1	87	35.2	44.4	94	no	0.377
means				28.9	37.8		31.8	39.6			
Aneides lugubris	29	♂	8.593	36.7	37.6	254	37.7	38.1	261	no	2.041
	32	..	3.745	37.6	31.6	172	38.3	31.9	177	no	0.736
	37	♂	3.545	31.0	33.0	132	31.0	33.0	132	no	0.807
	47	♂	5.822	31.0	30.9	179	31.9	31.3	185	no	1.242
	48	♀	5.637	33.0	34.4	198	33.7	34.7	203	no	1.297
means				33.9	33.5		34.5	33.8			
Aneides flavipunctatus	19[a]	..	3.966	36.9	35.0	186	36.9	35.0	186	yes	0.875
	38	♀	5.884	35.4	40.6	172	36.4	41.1	179	yes	1.537
	41	♀	5.327	31.8	40.1	138	32.5	40.5	143	yes	1.457
	45	♂	6.658	32.8	35.1	178	33.5	35.5	184	yes	1.547
	46	♂	3.581	34.0	34.3	117	34.6	34.6	121	yes	0.819
	49	♀	5.725	30.6	41.9	166	31.3	42.4	171	yes	1.667
means				33.6	37.8		34.2	38.2			
Aneides ferreus	28	..	3.117	36.0	35.5	117	37.1	36.1	123	yes	0.709
	43	..	0.713	34.9	31.5	58	37.6	32.8	63	yes	0.146
	44	..	0.986	33.3	34.0	55	34.3	34.6	59	yes	0.224
means				34.7	33.7		36.3	34.5			
Ensatina eschscholtzi	24	♂	4.880	40.6	33.9	164	41.9	34.7	173	yes	0.983
	25	♀[b]	3.946	42.4	37.5	186	43.6	38.3	192	no	0.852
	30	♀	5.455	33.7	37.2	138	33.7	37.2	138	yes	1.344
	31	♂	3.107	45.5	33.0	146	45.5	34.0	146	yes	0.577
	33	♂	2.726	34.8	33.2	111	34.8	33.2	111	yes	0.590
	34	♂	4.470	34.1	....	128	35.8	....	125	....	.....
means				38.5	35.2		39.2	35.5			
Plethodon elongatus	17[a]	..	4.054	34.8	33.9	182	....	....	.....	no	0.897
	27	♀[b]	3.111	27.3	35.1	89	29.0	39.9	96	yes	0.793
means				31.1	34.5		29.0	39.9			
Plethodon dunni	16[a]	..	2.903	20.1	28.2	66	....	....	...	no	0.655
Rhyacotriton olympicus	13[a]	♂	1.423	5.8	....	9	....	....	...	no	.....
	15[a]	♂	1.798	5.8	....	14	....	....	...	no	.....
	15[a]	♂	1.403	13.9	....	33	....	....	...	no	.....
	20[a]	♂	1.776	5.7	22.6	10	21.2	27.1	50	yes	0.379
	26	♂	1.713	5.7	24.6	11	17.7	27.9	40	yes	0.397
means				7.4	23.6		19.4	27.5			

depends upon total body water content which is variable. Some species differ as to the percentage of their bodies composed of water as Figure 3 suggests. The slimmer species of salamanders—notably *Batrachoseps*—generally have a lower body water content than the stouter species. Total body water content also differs between animals of different size, but of the same species. Such intraspecific differences are reported by Thorson (1955), the smaller individuals—in this

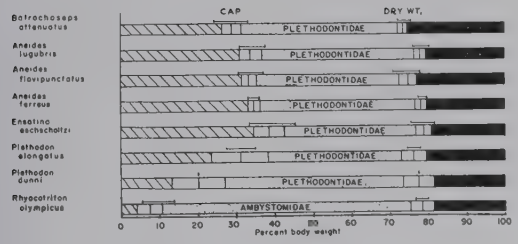

FIG. 3. Diagrammatic representation of the percentages of dry weight, of water that may be lost before the CAP is reached, and of water remaining in the body at the CAP. For explanation of CAP, see the text. Symbolism is the same as that used for Fig. 2.

case anurans—having a greater proportion of body water.

Shelford (1913) notes that during desiccation there is a period of "oversensibility"[5] followed by a period of over-stimulation ending in depression and fatigue. Among the salamanders studied, heightened sensitivity was manifested by increased efforts to escape which in the over-stimulation stage became vigorous and frantic. Depression and fatigue occurred just before death and ended in partial or complete paralysis which was almost always evidenced first in the hindquarters and proceeded forward. Two special reactions occurred within this general pattern. *Batrachoseps* and *Ensatina* both showed a tendency to lose the tail when intensely annoyed by the dry air. *Batrachoseps*, *Aneides lugubris*, and *A. flavipunctatus* were observed to secrete mucus in large quantities. A discussion of the reactions of each species to drying will be given in a following section. Whether or not the procedure killed the animals is indicated in Table I.

DISCUSSION

Tolerance of water loss. Thorson and Svihla (1943) and Littleford *et al.* (1947) demonstrated differences in the abilities of various amphibians to survive water loss, but statistical tests of the significance of their results were not made. Such an analysis is made here.

Thorson and Svihla show a correlation between dryness of habitat and the mean values for the percentage of weight loss at the lethal point. It is evident (Fig. 2) that, as was pointed out by these authors, intra-generic (species) differences are not indicated. An exception, perhaps, is *Rana grylio* as compared with other *Rana*. The genera used were from different families, thus only familial differences are indicated. Figure 2 shows that all the species of frogs and toads tested are essentially alike in body water content.

[5] Heightened sensitivity is perhaps a better description of the condition observed.

Littleford *et al.* (1949) show generic differences within a single family. Use of cessation of throat movements to indicate the lethal point may have been a factor in their low values, *i.e.* 18 to 25% water loss at this point. This method also gave a large range of variation, but the numbers of individuals in the samples were sufficient to yield statistically significant results. They show that *Eurycea* and *Desmognathus* which live in generally wetter environments than *Plethodon* are not able to survive as great water loss as the latter (Fig. 2). These species all have about the same water content.

My work (Fig. 3) indicates that differences in tolerance to water loss in salamanders occurs at the familial and generic and perhaps also at the species levels (*Plethodon*). In most instances, tolerance of water loss is directly correlated with the moisture conditions of the animal's environment; the drier the microenvironment, the greater the tolerance of desiccation.

It is apparent from Table I that slightly different tolerance pictures are given by the averages for the percentage of weight loss and the percentage of the body as dry weight at the CAP and LP. These two expressions of tolerance actually express two different things. The percentage of weight loss is related to the total body water available from the start of desiccation. The per cent of the body as dry weight at the CAP or LP is not related to total body water available, but is a physiological expression of how dry the tissues can become before death ensues. *Batrachoseps* and *Aneides flavipunctatus*, for instance, are physiologically the most able to endure the loss of body water, but since their total body water content is slightly lower than that of *Aneides lugubris* and *Ensatina*, the later species appear to be more tolerant in terms of the percentage of weight loss at the CAP.

In these three studies, amphibians are shown to have a range of tolerance from 7% to almost 50% weight loss (as water) before immobility or death occur. Hall (1922) desiccated several animals from various classes of invertebrates and tetrapods. Some of them possessed the ability to lose water as follows (figures represent weight lost as water): mouse (*Mus*) 34.0%, turtle (*Chrysemys*) 33.1%, lizard (*Anolis*) 46.3% lizard (*Phrynosoma*) 33.8%, lizard (*Sceloporus*) 47.8%. Some amphibians are as tolerant of water loss as the most tolerant of these, but others are much less so.

Surface-mass relationship and its relation to water loss rate. The smaller the mass of an animal, other things being equal, the greater its relative surface area will be. Since most of the water in plethodontid salamanders undergoing desicca-

tion is lost through the skin (there being no lungs), it would seem that the smaller the individual desiccated, the more rapid would be its rate of water loss per unit of mass. If so, in relation to this factor alone, large size would be of advantage for terrestrial life. There are, however, obvious disadvantages to large size—limitation in the use of places of retreat and a concomitant slowness of water uptake. Furthermore, Thorson (1955) has shown that the larger individuals of species of anurans have a lower percentage of their bodies as water.

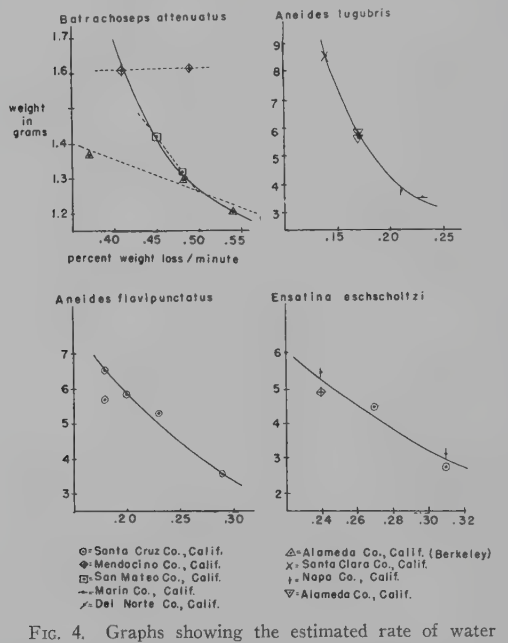

FIG. 4. Graphs showing the estimated rate of water loss in four species of salamanders of different sizes. The graphs show that there is a surface-volume relationship with respect to water loss from the skin. Each symbol represents a single individual which is identified as to locality of collection. With respect to *Batrachoseps*, it would be desirable to test this relationship further, using animals from the same locality.

Figure 4, plotting the percentage of weight loss per minute against the starting weight, shows that, in almost every instance, the larger individuals of the species had the slowest rate of water loss per unit of mass, while the smallest individuals had the fastest rate. The geographical location is indicated for each individual of each species tested in Figure 4. *Aneides lugubris* and *A. flavipunctatus* show good, hyperbolic, surface-mass curves. *Ensatina* also shows good fit to the curve with the exception of the individual from Del Norte County. This was a female with eggs. Perhaps her gravid condition and stout shape affected the desiccation rate. *Batrachoseps* shows very poor fit to a hyperbolic curve (solid line on the graph), but the individuals of this species came from three well-separated geographical areas and are too few to draw any conclusions as to the variability of the species.

Cohen (1952) found no clear correlation between salamander size and the rate of water loss, although he says that there is probably a surface-mass relationship which is obscured by behavior, skin differences, etc. I believe that this relationship was obscured by the apparatus he used—a jar-shaped desiccation chamber, the disadvantages of which are outlined above. He studied *Aneides lugubris, Ensatina eschscholtzi xanthoptica,* and *Taricha torosa torosa,* the first two of which are also considered in my work and do show the surface-mass relationship. Thorson (1955) also found a clear-cut surface-volume relationship in anurans.

Sexual differences. The percentage of the body as dry weight at both the CAP and LP for *Aneides flavipunctatus* and *Ensatina* differed as to sex (Table I). All females of these species tolerated greater water loss than the males. There is also some suggestion that female *Ensatina* have less body water content than the males. Thorson (1955) found no sexual differences with respect to tolerance of water loss in anurans.

Tolerance of water loss in relation to habitat. 1. *Batrachoseps attenuatus.* When on the surface of the ground, individuals of this species live in moist conditions under rocks, logs, boards, leaves, and other objects. They retreat underground in dry weather, but seldom, if ever, make burrows themselves. The elongated body shape allows them to use the borrows of worms, termite tunnels, root channels, and other cavities for retreat. Their small size and relatively extensive skin surface would not seem to suit them for living in dry places, but there is perhaps compensation in their ability to enter small openings and in their coiling behavior. Their immediate and excited attempts to escape in the experiments indicate that they are very sensitive to dry air.

2. *Aneides lugubris.* This species is found in trees and on the ground. Cohen (1952) reports that he found them several months after other species had retreated from the dry weather of late spring. I have found them in both moist and dry situations. This salamander and *Ensatina* seem to be the most tolerant of dryness of any of the species investigated. The thick skin, large size, and stout shape and especially the habit of hugging the substrate in a coiled position may explain

this tolerance. As Cohen points out, "hugging" of the surface on which they rest also enables them to absorb lost water quickly. Of all species studied, large individuals of this species had the lowest rates of water loss. This salamander can withstand considerable water loss, but not as much in terms of the percentage of the body as dry weight as *Batrachoseps*. Table I shows that all lived following desiccation, but some of those that lived never regained the full use of their hind limbs.

3. *Aneides ferreus*. This species, though more arboreal than *A. lugubris*, occurs in a more humid environment. It is an inhabitant chiefly of the redwood and Douglas fir forests of the northwestern coast, whereas *A. lugubris* is largely a species of the Lower Sonoran life-zone, closely associated with coast and interior live oaks. There is a tendency for this species to coil the tail. The salamander's protective behavior is otherwise close to that of *A. lugubris* although not as pronounced.

4. *Aneides flavipunctatus*. The subspecies *niger*, used in these experiments, is found upon or in wet soil in rocky situations along streams, in talus where seepage occurs, or in damp situations not far from water. It is found in much wetter situations than *A. lugubris, Batrachoseps,* or *Ensatina*. It has equal tolerance of water loss to *Batrachoseps* in terms of the pecentage of the body as dry weight at the CAP. The thin skin, sensitivity to drying, and lack of protective habits, such as coiling, indicate an animal adapted to wet situations.

5. *Ensatina eschscholtzi*. Of the habitat, Stebbins (1951) says: "Greatest concentrations of individuals are likely to occur on flat or gently sloping benches, above flood level, rather than on steep slopes. A perennial stream is often present although it is not a necessity, since individuals have been found miles from water." The species showed no special protective behavior when in the experimenal chamber. During desiccation a typical posture is one with the body held high off the ground with head and tail extended. Annoyance with dry air was sometimes evidenced by the exuding of a white secretion from the granular glands of the tail. This salamander can withstand considerable water loss in terms of the percentage weight loss, as great or greater than any salamander studied.

6. *Plethodon elongatus*. This species occurs in stabilized rock slides or, less commonly, under boards, bark, or other litter overlying moist soil. It showed rapid drying and a sensitivity to dry air, resembling *Batrachoseps* in its tolerance of water loss. In the experiments, it showed no special protective behavior.

7. *Plethodon dunni*. This is a species which, in general, lives in much wetter situations than does *P. elongatus*. A saturated substratum characterizes its niche. The single individual tested exhibited a low resistance to drying and showed no special protective behavior. There was extreme irritation on contact with dry air and rapid desiccation.

8. *Rhyacotriton olympicus*. This is the most aquatic of all the species tested. It is found commonly in or near small, cold, clear, permanent streams. The low tolerance of water loss, great irritation on contact with dry air, rapid desiccation, and lack of any protective behavior correlate with this habitat.

Conclusion

The ability to survive increasingly great losses of body water, other things being equal, means that animals adapting along such lines have more time in which to reach more suitable habitats or to await the return of favorable moisture conditions when they are subjected to desiccation. Such an adaptive trend would seem to be of special importance to animals living in places subject to periodic drying or to generally increasing aridity. Increased tolerance would allow for more extensive wandering, favoring extension of range both of the individual and of the species, or for a better chance of survival during a period of low humidity. Increased tolerance by itself probably does not mean that the amphibian is therefore able to live in a dry situation. All amphibians will eventually desiccate even in saturated air. Water must be available. But in emergencies, when the animal is caught in a drying location this factor plus protective behavior (such as coiling) and increased skin thickness may mean the difference between life and death.

The recent papers by Thorson (1955 and 1956) indicate that the rate of desiccation in frogs is not constant, contrary to what had been generally believed. He shows that, during desiccation, "a comparatively brief initial reduction in the rate of water loss was followed by an extended period of more rapid dissipation of water than occurred in dead animals." He questions the survival value of these rate changes and asserts that the "changes in rate were not primarily of a water conserving nature." I believe that Thorson's emphasis on the later "rapid dissipation of water" rather than on the "initial reduction in the rate" is misdirected, particularly since he was also able to show that repeated desiccation performed on the same animals in some cases increased the ability of the animal to slow the rate of water loss. There is, as he says, the probability that water loss is partially

controlled and adjusted through the action of the deeper tissues.

It is probable that both short-term and long-term adjustments in water loss rate have definite survival value and are widespread in amphibian species and that the initial reduction in the rate is of a water-conserving nature in the natural environment of the amphibian. The heightened sensitivity which amphibians show at the onset of desiccation, when they are first exposed to dry air, might bring on an immediate adjustment to slow the rate of water loss in nature (where the animal is not restricted as it is in a test desiccator and where environmental conditions undergo more subtle change than in the laboratory). Therefore, the "initial reduction" and the long-range adjustment to repeated desiccations are the important adaptations, while the "extended period of more rapid dissipation of water" may well be of little consequence in nature where an amphibian might never reach this state.

An animal's ecological preference is due to a combination of many factors. It is obvious that only one factor need differ between two species to result in different habitat preferences and it is equally obvious that different species adapt to similar environments in different ways. *Aneides lugubris* and *A. flavipunctatus niger* differ strikingly in skin thickness and in their behavior when subjected to desiccation. The thin skin of the latter would seem to preclude the possibility of this salamander's living in a relatively dry microenvironment. The well-developed protective behavior, thick skin, and large size of the former are probably important characteristics making it possible for this salamander to live in the driest microenvironment of all species studied despite the fact that it may not tolerate loss of body water quite as well as *Ensatina* which lives in a wetter microenvironment. The slender shape, small size, and relatively large skin surface of *Batrachoseps* is offset by the ease with which it is able to find openings into which it can escape from dry conditions. *Batrachoseps'* low percentage of total body water is also offset by the great tolerance of desiccation in terms of the percentage of the body as dry weight at the CAP. *Ensatina*, on the other hand, compensates for a comparative lack of protective behavior by having the most well-developed tolerance to water loss of all species studied (in terms of the percentage weight loss).

Summary

Present and earlier work show that the ability to survive water loss is roughly correlated with environment. The greatest loss is generally tolerated by those species that live in the driest habitat. This correlation is evident at the family level, less evident at the generic level, and, so far as present studies go, only occasionally present at the species level. Various species of amphibians show a range of water loss tolerance of from 7 to almost 50% in terms of the percentage of their total weight lost during desiccation. This figure of 50% indicates as great a tolerance as is shown for any vertebrate, but the existence of less tolerant species emphasizes the transitional position of the Amphibia from aquatic to terrestrial forms.

There is a surface-mass relationship with respect to rates of water loss in Amphibia, the highest rates of loss per minute being found in the smallest individuals of a species.

The data suggest that some female salamanders may have greater ability to endure water loss than the males. The percentage of total body water may be less in the females of some species than in the males. The slimmer species of salamanders appear to have a smaller percentage of total body water than the stouter species.

The ability to tolerate water loss is only one of the many factors involved in survival and, from the point of view of salamander ecology, can be correlated only roughly with environmental occurrence. Skin thickness, body size, and various behavioral mechanisms as well as physiological adjustment of the rate of water loss from the skin, a phenomenon recently discovered by Thorson, are the most important of the other factors that permit life in dry places. All these mechanisms interplay, some acting as compensating mechanisms for others, depending on the particular adaptations of the species in question. The chief value of tolerance of water loss and of a reduction in the rate of desiccation would seem to be in allowing for a somewhat longer escape period when the animal is faced with drying conditions or a longer period of tolerance of marginal moisture conditions. Tolerance, by itself, cannot insure life in dry places since all amphiibans will eventually desiccate without a supply of water being made available to them.

Various improvements of technique are discused as follows: (1) a tubular chamber used for desiccation which reduces tolerance of circulating air; (2) an improved method of determining the leathal point involving the loss of the righting reaction and indicating a point named the Critical Activity Point (since it is close to, but not identical with, the true lethal point); (3) two methods of representing the lethal point, one of which simply gives the percentage of the body weight lost (as water) and the other of which gives the percentage of the body as dry matter at the lethal

point (a physiological expression of the water content of the tissues at death).

The species used in the experiments are discussed with respect to their reactions to desiccation and their habitats.

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STRATIFICATION OF ARTHROPODS IN A WET STUMP CAVITY

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Few workers in the United States have investigated the arthropod populations inhabiting wet stump holes. Generally, only restricted groups or individuals have been reported from such cavities. In 1861, Benjamin Walsh observed the larvae of an helodid beetle, *Prionocyphon discoideus* Say, in a stump hole near Rock Island, Illinois, and communicated his detailed findings to Osten Sacken (1861). A puparium of the syrphid *Criorhina pictipes* was reported from a stump hole in Virginia by Greene (1923). He also found species of several other genera in moist tree cavities. Jenkins and Carpenter (1946) have compiled records of tree hole mosquitoes some of which also breed in wet stump holes. While studying the breeding sites of tabanids in the Yazoo-Mississippi Delta, Lewis and Jones (1955) found larvae of *Leucotabanus annulatus* Say to occur commonly in willow stumps, particularly those surrounded by coppice. During the past two years random observations have been made on arthropods found in a wet stump hole near Town Creek, Alabama. It is the purpose of this paper to identify these individuals and to consider their position within the microhabitat.

Habitat Conditions

The tree stump was situated among smartweed and buttonbush at the outer margin of a limesink called Meadow Pond about a mile north of Town Creek, Alabama (Fig. 1). The portion of the sink about the stump was intermittently flooded to a depth of several inches, but the ground water table did not affect the water level within the stump. The original tree, a sweet gum (*Liquidambar styraciflua* L.), was cut down several years ago leaving a stump approximately 30 in. high and 26 in. in diameter with a hole in the middle about 16 in. across at the top. In the interior of the stump some heartwood persisted on the east side, but only pulpy sapwood remained on the west side in the dry wall portion. Coffee-colored water that was retained in the base during most of the year had a depth of over one foot in the spring but was considerably lower in the fall. With the exception of certain mosquitoes, the larval forms of aquatic Diptera present were able to pass the fall dry period in moist, woody debris at the base of the cavity.

Portions of the interior of the stump roughly including the north wall and adjacent water surface were reached by direct sunlight during midday hours in summer. Midday temperatures (° F) taken during visits in 1956 were as follows:

	April 25	*May 19*	*June 8*	*June 30*	*August 7*
Dry Wall	69	84	78-80	83	93-94
Water	57-59	71	75	83-85	83-84

One nighttime temperature reading on July 3, 1956, at 0230 hours suggests a slight dropoff overnight with wall temperature at 79° F and water temperature at 75° F. Air temperatures recorded

FIG. 1. Sweet gum stump at edge of Meadow Pond, Town Creek, Alabama, used in observations on stratification of arthropod populations, August 10, 1956.

at Muscle Shoals, Alabama, from October 25, 1955, through March 1956 show the number of days with temperatures below freezing as follows: October —1; November —12; December —15; January —20; February —5; and March —8. Minimum temperature of 14° F was reached on December 16, 1955.

PROCEDURE

As a rule samples of wood and stump hole water were returned to the laboratory for rearing of immature insects. Pupae and puparia were removed for individual rearing in order to associate cases and exuviae with the respective imagoes. Isolation of puparia was also useful in detecting hymenopterous parasites of syrphids.

Temperature readings were made from shaded areas on the wall, at the water surface, and several inches below the water surface. Because several local curiosity seekers were roused by visits of the investigator to explore the stump and environs, it was deemed advisable to omit the use of continuous recording devices for climatic measurements. During the last two months of the investigation much of the stump was torn away at the bottom allegedly by such individuals, but the water-retaining capacity of the stump hole was unimpaired.

Wood samples were taken in August 1956 from various areas of the inner wall for determination of moisture content. Five-gram samples were weighed, dried in an autoclave at 110° C for 24 hours, and then reweighed to determine moisture content by per cent.

WET STUMP HOLE FORMS

As in wet tree holes, the inhabitants of the wet stump hole can be readily grouped or separated by their relationship to the water mass. These groups or forms may be considered as follows: wall forms, surface or surface ring forms, subsurface or aquatic forms, and pedonic forms associated with subsurface ooze and debris according to Snow (1949). In addition to the groups mentioned above, subcortical forms were also noted. While both terrestrial and aquatic microseres were operative in the wet stump hole, the presence of shelf fungi added a conk microsere which could not be studied because of its recent appearance. Park *et al.* (1950) have discussed the role of fungi in tree hole microseres.

DRY WALL FORMS

Generally speaking the inner wall of the wet stump hole harbored a small population in the upper drier portion and a large population in the moist wood from the water's edge upward, downward, and inward (Fig. 2). In the stump hole investigated the dry wall forms were those occurring in pulpy wood about 10-14 in. above the water surface where the moisture content varied from about 10% to 20%. On March 24, 1956, five serropalpid beetles, *Eustrophinus bicolor* (Fab.), were found an inch beneath dry pulp in the wall with several foraging ants, *Aphaenogaster*

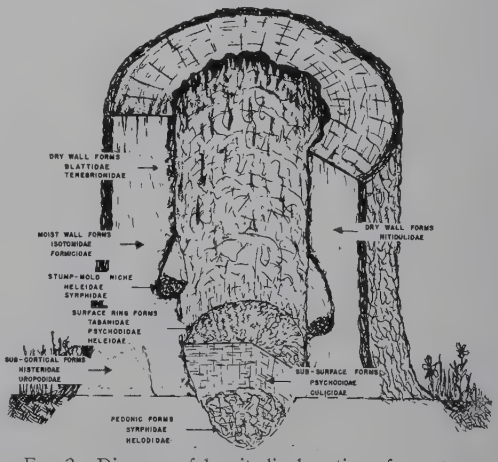

FIG. 2. Diagram of longitudinal section of sweet gum stump at Meadow Pond, Town Creek, Alabama, 1955-1956, indicating location of principal arthropod families.

lamellidens Mayr. Occasional wood roaches, *Parcoblatta* sp., were also noted as on all other visits. Several orange and black nitidulids were seen crawling in crevices May 12, 1956, but could not be captured. Adults of the mosquito *Aedes triseriatus* (Say) were resting in crevices on May 19, 1956, and occasional black ants, *Ponera coarctata pennsylvanica* Buckley, were crawling about the wall. On June 8, a tenebrionid, *Platydema ruficorne* Sturm., was found with five dermestid larvae in the dry pulp.

Moist Wall Forms

The moist wall forms were found in stump hole mold and fairly intact sapwood varying from about 30% to 73% in moisture content. Those individuals occurring nearest the inner wall (within 2 inches) are cited here, whereas those nearest the outer wall of the stump will be mentioned with the subcortical species. Moist wood of the inner wall exists over a vertical gradient well above and below the water level in the base of the stump. For practical purposes collections of arthropods were limited to the moist wall above the existing water surface and the wet wall at the water surface (surface ring). In prolonged dry periods capillarity often permitted wetting of the wall several inches above the existing water level. Collections from the upper portion of the moist wall approximating the area inhabited by those listed under dry wall forms will be described first. The first collection on March 18, 1955, revealed only one large carabid, *Loxandrus parallelus* Casey. On September 19, 1955, beetles including the following were captured: *Eucinetus morio* LeC. (1) (Eucinetidae), *Dioedus punctatus* LeC. (3) (Tenebrionidae), *Conosoma* sp. (1), *Coproporus* sp. (1) (Staphylinidae), *Epierus pulicarius* Er. (1) (Histeridae), *Tachyura capat* LeC. (1) (Carabidae), and *Baeocera* sp. (1) (Scaphidiidae). Two pseudoscorpions, *Verrucaditha spinosa* (Banks) (Tridenchthonidae) and *Pselaphochernes parvus* Hoff (Chernetidae), were also individually represented. The first collection in 1956 on March 24 revealed a nearly mature larva of *Leucotabanus annulatus* in the upper portion of the moist wall and an adult of the eyed click beetle *Alaus oculatus* (L.) (Elateridae). A nest of the ant *A. lamellidens* was uncovered at a point intermediate in position from the dry wall zone and the water surface and about 2 in. inside the wall. It contained about 30 workers of both sizes. Also present in the nest area were two collembolans, *Isotoma sensibilis* Tullb. (Isotomidae) and *Pseudosinella candida* Fols. (Entomobryidae), the former being very abundant. The following individuals, with emergence dates, were reared from this site in the laboratory: 3 *Coenosia basalis* (Stein) (Muscidae), 3-30-56, 4-1-56; 1 *Zelmira* sp. nr. *mendica* (Lw.) (Fungivoridae), 4-28-56; 3 *Bradysia* sp. (Lycoriidae) 4-28-56; 2 *Ptinella* sp. (Ptiliidae), 4-28-56; and 1 *Thesium cavifrons* (LeC.) (Pselaphidae), 4-26-56. Eggs of a gryllid, *Acheta* prob. *assimilis* F. (s. l.), taken between thin layers of moist wood on March 24, 1956, had hatched, and nymphs (3) had reached the second instar by April 17, 1956, when the specimens were preserved. On April 25, 1956, when this intermediate zone was revisited, no *Aphaenogaster* were seen, but aquatic larvae (6) of an helodid beetle, *Prionocyphon discoideus,* had migrated to this site from the water to pupate. Adult beetles found in the moist wall at this time were *Conosoma* sp. (1), *Coproporus* sp. (1), *E. pulicarius* (2), and *T. cavifrons* (1). A large bluish collembolan, *Isotoma viridis* Bourl., was also present. Two males and one female *Dasyhelea oppressa* Thoms. (Heleidae) emerged from retained wood in the next four days. On May 12, 1956, collections beneath two inches of wood in the upper portion of the moist wall revealed single specimens of the horned passalus *Popilius disjunctus* (Ill.) (Passalidae), the ant *A. lamellidens,* and a female pseudoscorpion, *Parachernes* sp. On May 19 the same position was sampled and the following collembolans recorded: *Pseudachorutes subcrassoides* Mills (3) (Poduridae), *Xenylla welchi* Fols. (1) (Poduridae), *Lepidocyrtus cyaneus* Tullb. (2) (Entomobryidae), and *Pseudosinella candida* (1). One specimen of an endomychid beetle, *Rhanis unicolor* Ziegl., and the pseudoscorpion *V. spinosa* were also found. A single *Aphaenogaster* was seen on the moist wall on May 19; however, when revisited on June 30 approximately 30 specimens were roused from the nest in the moist wall. At the upper end of the moist wall zone and several inches within the wall, two empty puparia of a short-tailed syrphid, *Milesia virginiensis* (Drury), were discovered on June 30. Of the syrphids ordinarily encountered in stump holes and tree holes, *Milesia* appeared to be the least aquatic and its appearance in the upper portion of the moist wall was expected. During the summer of 1955, a female *Milesia* was noted ovipositing in crevices on the inner wall about 8-10 inches above the water surface.

Stump Mold Niches

The stump mold niches were small depressions on the moist inner wall of the stump cavity and contained varying amounts of fine-grained stump mold derived from the immediate wall or from falling particles. These niches were naturally subject to more extreme wetting and drying than

the inner portions of the moist wall zone. However, because of their proximity to the water surface, they were usually quite moist, at least in the bottom of the niche, and did not appear to range much below 70% in moisture content. In 1955, puparia of the syrphid *Milesia virginiensis* were first collected on May 4, with several adults emerging on May 12. Two additional puparia of *M. virginiensis* taken on May 23 emerged on May 25 and May 27, respectively. On May 15, puparia of *Meromacrus acutus* Fab., a large, long-tailed syrphid, were removed from niches and emerged on May 18 and May 21. A third species of Syrphidae, *Eristalis transversus* (Wied.), was present as a pupa on May 15 and emerged on May 21. One niche sampled on July 8 yielded about 20 larvae and pupae of *Forcipomyia bipunctata* (L.) (Heleidae). Also present was a tabanid larva, *L. annulatus,* which later pupated and emerged on July 20. A larva of the cranefly, *Teucholabis immaculata* Alex., also collected on July 8, pupated and emerged in the laboratory by July 31. During a visit to the stump hole on September 19, 1955, a puparium of what is thought to be *Eristalis transversus* was found in a moist niche and returned to the laboratory for rearing. Two days later, about 50 mixed adults of the genus *Trichopria* (Diapriidae) issued from the puparium in the region of the dehiscent plates. According to Muesebeck (corresp. 1955), they are typical hymenopterous parasites of Diptera always issuing from the pupa or puparium. Due to heavy sampling of the stump mold niches in 1955 only one pocket about 2 in. deep and approximately 6 in. above the water surface was suitable for sampling in 1956. On June 8, a single large tabanid larva, *L. annulatus,* and a puparium of *Meromacrus acutus* were present, the latter species emerging on June 13, 1956.

Surface Ring Forms

A considerable congregation of aquatic and semi-aquatic forms occurs where the water level meets the inner wall of the stump cavity. The upper extent of the ring is determined by the degree of capillarity. In the stump studied, the band of inner wall surface just above the surface film affected by capillarity was considered to be about one inch vertically. The position of the surface ring naturally varies slightly up and down on the inner wall due to periodic addition of rainwater and the depleting effects of evaporation. Moisture content along the surface ring varies from about 75 to 90% and higher. Persistence of fibrous elements of the heartwood on the inner wall adjacent to the water provides for the retention of small pockets of wet mold in a discontinuous circular zone behind the existing surface ring. Actually these small pockets are submerged or partially submerged stump mold niches. When the wet zone immediately behind the surface ring was first examined on March 24, 1956, several larvae of *Leucotabanus annulatus* were discovered (laboratory rearing produced adults on May 12, 13, and 14). Lewis and Jones (*op. cit.*) have noted *L. annulatus* to occupy a similar position in willow stumps. Another larva of *L. annulatus* and a larva of *Meromacrus acutus* were found beneath woody debris just above the water line on an emergent piece of wood in the water. Larvae of the psychodid *Brunettia nitida* (Banks) were numerous in the surface ring on March 24. A sample of wet wood from the surface ring retained in the laboratory until April 10 produced heleid adults of *Dasyhelea oppressa* (14) and *Culicoides arboricola* R. & H. (4), psychodids, *B. nitida* (2) and *Telmatoscopus superbus* (Banks) (1), and an undetermined tendipedid species of the genus *Hydrobaenus* (4). Collembola frequenting this ring on March 24 were *Isotoma viridis* (2). The next visit on April 25 showed *B. nitida* (2), *Culicoides guttipennis* (Coq.) (4), *Hydrobaenus* sp. (3), and *A. triseriatus* (4) present in the late larval or pupal stages. On May 12 larvae of *L. annulatus* (1) and *D. oppressa* (11) were found in a wet pocket behind the surface ring. One puparium of *M. acutus* from this pocket emerged on May 22. Predators, *Acheta* prob. *assimilis* and the pseudoscorpion *Verrucaditha spinosa,* were also present. Two additional puparia of *M. acutus* occurred behind the surface ring on June 8 with emergence on June 13. A recently emerged male helodid, *P. discoideus,* was also noted. One second stage larva of *M. acutus* was taken in a wet pocket on June 30. A final inspection on August 7, 1956, showed 4 pupae of the psychodid *B. nitida,* 2 pupae of *C. arboricola,* and a pupa of the heleid genus *Atrichopogon* present in a three-ounce sample from the surface ring.

Subsurface or Aquatic Forms

The coffee-colored open water in the base of the stump served as a medium for the immature aquatic stages of certain Psychodidae, Heleidae, Culicidae, Syrphidae, and Helodidae. With the exception of the mosquitoes, the other groups represented were able to continue activity even when water had evaporated until only wet debris was present. During the winter the larvae of psychodids, heleids, syrphids, and helodids remained quiescent in ooze and debris beneath the water and ice. On March 24, 1956, water temperatures were still in the low 50's and the main

activity of aquatic larvae was in the surface ring. By April 25, many second stage and a few fourth stage larvae of *Aedes triseriatus* were present in the water with numerous mature larvae and pupae of *Brunettia nitida*. Again on May 12, larvae and pupae of *A. triseriatus* and *B. nitida* were encountered in the water. Water samples showed larvae of *B. nitida* present on May 19 and pupae of *A. triseriatus* on June 8. No larvae of *A. triseriatus* were found on July 3, but two other mosquitoes had invaded the stump. Mature purple-pigmented larvae of *Orthopodomyia signifera* (Coq.) averaged about 7 per dip with an ordinary drinking dipper. Mature larvae of the predaceous and cannibalistic *Toxorhynchites rutilus septentrionalis* D. & K. were also recovered at about 1 per dip in 4 dips. One pupa of the heleid *Culicoides arboricola* was also collected at the water surface. During a final visit on August 7, larvae of *O. signifera* were still abundant but only one pupal exuvium of *Toxorhynchites* was noted.

Micropedonic or Subsurface Bottom Forms

An ooze layer interspersed with bits of fallen stump mold in various stages of decay is present in the base of the stump beneath the water. During the first visit to the stump hole on March 18, 1955, mature larvae of *M. acutus* (10-12) were found in ooze on the bottom along with many large larvae of *P. discoideus* which were actively crawling about submerged pieces of wood. Two nearly mature larvae of *M. acutus* were recovered at the bottom on July 8, 1955. Larvae of *P. discoideus* (15+) were very active on submerged wood when the stump was visited on March 24, 1956. On April 25, a large larva of *M. acutus* was taken from submerged wood with 20 *P. discoideus*. The *Meromacrus* was returned to the laboratory but did not emerge until August 10. Small numbers of *C. guttipennis* were also present on April 25.

Subcortical Forms

During the course of the investigation the stump has gradually been divested of bark. In 1955 only one casual observation beneath bark revealed an adult of the eyed click beetle *Alaus oculatus*. On May 19, 1956, bark was removed from the base of the stump and mold with moist grass was returned to the laboratory. Later sampling of this site showed the mold to have a moisture content of 84.1%. A variety of mites, collembola, and beetles was found in a 16-ounce sample taken on May 19. The following Coleoptera were present: *Aeletes simplex* LeC. (1) and *Bacanius punctiformis* LeC. (5) (Histeridae), *Thoracophorus costalis* Er. (1) and *Sciocharella delicatula* Casey (2) (Staphylinidae), and *Connophron* sp. nr. *fulvum* LeC. (1) (Scydmaenidae). The collembola were *Xenylla welchi, Pseudachorutes subcrassoides, Lepidocyrtus cyaneus* var. *cinereus* Fols. and *Isotoma cinerea* Nic. The pseudoscorpion *V. spinosa,* and numerous mites in the genera *Galumna* (Galumnidae), *Liroaspis* (Liroaspidae) and *Fuscuropoda* (Uropodidae) were present.

Discussion

Members of the Helodidae, Syrphidae, Culicidae, Heleidae, and Psychodidae encountered in the wet stump hole at Town Creek offer good grounds for comparison with typical inhabitants of wet tree holes in the area. Of the helodids known from wet wood, only *Prionocyphon discoideus* was present in the exposed stump hole. It appears to prefer large cavities in stumps and trees with much mold beneath the water surface. On the other hand, larvae of *Helodes fuscipennis* Guer. and *Helodes pulchella* Guer. are more frequently encountered in dark cavities with leafy debris and often some soil acquired by flooding or wind action.

Larvae of Syrphidae, especially *Meromacrus acutus,* were well represented in the stump hole. At New Orleans, Louisiana, *M. acutus* was taken from dark water in a camphor tree with *H. pulchella*. While *Eristalis transversus* may have invaded the tree cavity in response to small amounts of animal waste which is usual for members of the genus, only two specimens were noted. The absence of *Myiolepta pretiosa* Hull, or as Fluke and Weems (1956) consider it *Miolepta varipes* Loew, from collections in the stump hole is worth mentioning. This species is by far the most frequent syrphid in tree holes over north Alabama and Tennessee. Larvae mature readily in cavities filled with much wet mud as well as in situations with open water and abundant mold beneath. The only short-tailed syrphid collected in the stump hole was *Milesia virginiensis*. The larvae and puparia are usually encountered in the moist wood. However, several larvae were observed suspended from the water surface and feeding below the surface in a wet stump hole at Wilson Dam, Alabama.

Larvae of the mosquitoes *Aedes triseriatus, Orthopodomyia signifera,* and *Toxorhynchites r. septentrionalis* which occurred in the stump hole are regularly found in tree cavities in Alabama and Tennessee. Larvae of *Anopheles barberi* Coq. and *O. alba* Baker are also known from tree holes in the region but are infrequently encountered. Adults of *Anopheles quadrimaculatus* Say and *Anopheles walkeri* Theo. are known to use stump

holes as diurnal resting sites in this area but do not breed in tree hole cavities.

Larval representatives of the family Heleidae which live beneath the water of tree holes in Alabama and Tennessee are *Culicoides arboricola, C. guttipennis, C. nanus* R. & H., and *C. villosipennis* R. & H. The first two species were found in the stump hole and it is improbable that the latter two species would not normally be found there. Two other heleids, *C. hinmani* Khalaf and *C. paraensis* (Goeldi), which occur in moist, but not wet, cavities in Alabama and Tennessee were also absent at Town Creek. Larvae and pupae of *Dasyhelea oppressa* found in the surface ring of the stump are very common in the moist walls of wet tree holes.

The psychodid *Brunettia nitida* was one of the dominant species of aquatic Diptera taken from the wet stump hole. In tree holes it also prefers large wet cavities with much organic mold beneath the surface and may also be associated with *Telmatoscopus superbus*. Larvae of *T. albipunctatus* (Will.) are occasionally taken in cavities with leafy debris and in artificial containers with polluted water, but they did not appear in the stump hole.

The larvae of a large black and orange marked mydas fly, *Mydas clavatus* Dr., were not found in the stump at Town Creek. They are frequently found in decaying stumps in this region and have been observed beneath bark in an old oak stump at nearby Wilson Dam, Alabama.

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Summary

Observations of a sweet gum stump near Town Creek, Alabama, in 1955 and 1956 showed that the arthropod inhabitants could be segregated into dry wall forms, moist wall forms, surface ring forms, subsurface or aquatic forms, micropedonic or subsurface ooze forms, and subcortical forms.

In the dry wall, wood roaches, serropalpid beetles, and tenebrionid beetles were found. Dominant moist wall representatives were the ant *Aphaenogaster lamellidens* and a collembolan, *Isotoma sensibilis*. Stump mold niches formed suitable breeding sites for the heleid *Forcipomyia bipunctata* and served as pupation sites for the rat-tailed syrphids *Meromacrus acutus* and *Eristalis transversus* and the short-tailed *Milesia virginiensis*. The heleid *Dasyhelea oppressa* and the tabanid *Leucotabanus annulatus* were common in the surface ring area. Typical mosquitoes in water at the base of the stump were *Aedes triseriatus, Orthopodomyia signifera,* and *Toxorhynchites rutilus septentrionalis*. In the subsurface layer of ooze, larvae of an helodid beetle, *Prionocyphon discoideus,* and *M. acutus* were frequently present; however, both species migrated to moist areas of the stump wall for pupation and emergence. In subcortical situations, species of mites in the genera *Galumna, Liroaspis,* and *Fuscuropoda* were very abundant.

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A FURTHER EXAMINATION OF THE DISTRIBUTION OF THE BRUSH POSSUM, *TRICHOSURUS VULPECULA*, IN TASMANIA

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The Brush Possum, *Trichosurus vulpecula* (Kerr) is widely distributed in Tasmania as well as on the Australian continent, the species being polymorphic, exhibiting several colour varieties. Le Souef (1915) found on the mainland of Australia three colour phases of this species, namely a more or less rufous, a black and a fawn variety. He states that albinism is fairly common in the species and gives certain notes regarding the distribution of the colour phases.

Two colour phases of *Trichosurus* can be recognized in Tasmania; the most common phase is grey but black coloured individuals are frequently encountered. Both phases often show a more or less rufous tinge. The distribution of these two colours has attracted scientific attention. Pearson (1938) discussed the distribution of the two colour phases of *Trichosurus* and found that there was no apparent correlation between the distribution and either the rainfall or the topography. Huxley (1938, 1942 and 1955) also discussed this and the distribution of other melanistic species. He found that, in general, the darker phase became more frequent in areas where low temperature and low insolation are combined with high humidity and high rainfall.

Gerschenson (1945a and 1945b) examined the distribution of the colour phases of the hamster (*Cricetus cricetus* L.) in the Ukraine and has shown that black hamsters are the more plentiful in regions of greatest humidity. He has also shown that the percentage of blacks is greater in areas of high population and that there is a seasonal variation in the number of blacks in any one area.

The Brush Possum, in common with most marsupials, is nocturnal in habit, spending the daytime sleeping in trees. The animals spend some time on the ground at night and this habit has made it possible to catch them fairly easily by means of snares, the pelt of this species forming a valuable part of the Tasmanian fur industry. The structure and statistics of this industry will be described elsewhere. The present paper is based on data derived from the fur industry returns. This method of studying distribution is by no means new, having been practised for many years by both American and Canadian workers.

The nomenclature used follows that of Iredale and Troughton (1934).

METHODS

Four species of Tasmanian marsupials are trapped for their skins and royalties are payable on the pelts. The royalty is paid at a police station and a receipt is issued which shows the number and type of skins on which royalty was paid, and the locality in which the skins were taken. If the details on such a receipt are correct and based on reliable information, the receipts provide a means of estimating the distribution of any economically exploited marsupial.

The black and grey color phases of *Trichosurus* are of sufficient economic importance to justify separate entries on the royalty receipt. Examination of these receipts makes it possible to plot a distribution curve showing frequency of either colour phase.

The duplicates of the royalty receipts are forwarded to Police Headquarters in Hobart, and we are indebted to Mr. Shirley of the Police Department for giving us access to these returns. Any one police station may have skins brought to it from a large area containing many ecological types of country and a large number of the records obtained from the royalty receipts do not give sufficient information as to locality of capture. These have to be discarded. However, it is possible to use more than one-third of the records of any one trapping season (see Table I).

TABLE I. The number of skins taken in the open seasons 1949 and 1952

	Year	Black	Grey	Total
Number bountied....	1949	22,792	68,023	90,815
Number included in present survey.....	1949	11,988	23,250	35,238
Number bountied....	1952	18,186	43,171	61,357
Number included in present survey.....	1952	6,877	17,510	24,386

It should be noted that the percentage of blacks utilized for 1949 is greater than the percentage of greys, though this position is reversed in 1952.

The frequency of the percentage of blacks was plotted on a graph and suitable figures at which phenocontour lines could be drawn were selected. These figures are 25%, 55%, 75%. The tables upon which Figures 1 and 6 are based have been deposited in the Library of the University of Tasmania.

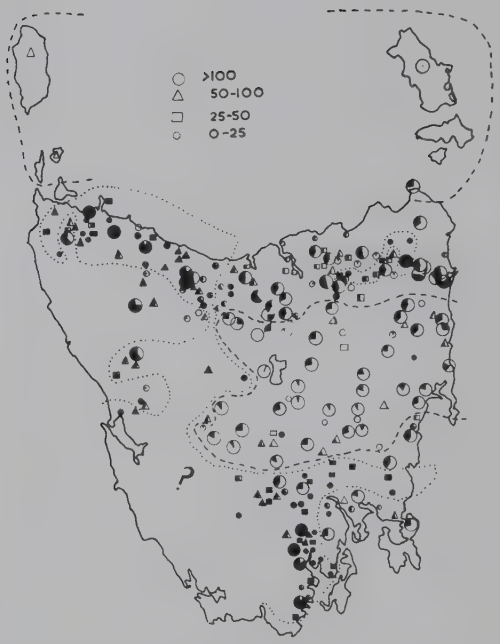

FIG. 1. The distribution of the two colour phases of *Trichosurus* in Tasmania. Areas of high percentage greys are within the broken line and the high percentage black population areas are within the dotted line. Mixed colour populations occupy the rest of the State. The symbols also show the proportion of blacks.

DISTRIBUTION OF THE SPECIES

The distribution of the black and grey phases is shown on Figure 1. The grey phase is more common on the East Coast and in the central Midlands region, while the black variety is found in the North-west, West and South coasts as well as in a small area in the North-west. Black Possums are not found on either Flinders or King Islands though there is a small black population on Three Hummocks Island. There are no data for most of the South-west area. An important feature of the distribution of *Trichosurus* is the area of high percentage of blacks running across South-eastern Tasmania to the East coast above the Forestier Peninsula. This area is based on statistically valid data as the samples are all strong. As additional evidence it may be stated that one of us (E.R.G.) has examined 90 skins from this area and these were nearly all black. We propose to call this area the Buckland-Nugent Pocket.

Tasmania can be divided into Possum distribution areas, each area being based on the relative numbers of the colour phase of the possum. These areas are as shown in Table II.

All of these areas are separated from each other by transitional zones of mixed population. The Western and Southern areas are probably one continuous area but lack of data from the unpopulated south-western part of the country, which is uninhabited by humans, prevents confirmation of this.

TABLE II. Possum distribution areas in Tasmania

Area	Percentage of black possums
North western	75–100%
Northern	25– 55%
Blue Tier	55– 75%
Western	75–100%
Southern	75–100%
Midland-Eastern	0– 25%
Flinders Is. & King Is.	0– 20%

In all cases the transitional region between high percentages of one phase to that of the other is very narrow. In this feature the distribution of the Possum colour phases follows that of the hamster as shown by Gerschenson (1945a) who found similar narrow transitional regions. The boundaries between high percentage black and high percentage grey on the North Coast is not as sharp as in the other parts of the country, due to the very variable vegetation of that region of Tasmania, where there are thick forest patches, intermingled with pastoral and agricultural areas.

It should be noted that the area of distribution of the black Possums is continuous in Tasmania. Although there are no figures available from the Tasman Peninsula for the 1949 and 1952 hunting seasons, Pearson (1938) recorded 17% black possums from Port Arthur at the southern end of the Peninsula. The Possum is also widespread throughout the State, there being no geographical or topographical boundaries to its distribution. It might be expected that the high mountainous midland area would act as a barrier to the species but this is not the case. However, the range of the species is limited by vegetational factors, since treeless areas do not support a Possum population. Such areas are very local in Tasmania and cannot affect the overall picture of possum distribution. In this connection it should be noted that clusters of trees, often isolated from forest areas by large paddocks or pastures, nearly always support a Possum population. This indicates the extent of the Possum's habit of roving on the ground. Trappers state that the Brush Possum moves for miles in migrations though we have no scientific proof of this statement. The black hamster in the Ukraine is similarly unrestricted by geographical or topographical boundaries (Gerschenson 1945a).

Using the catch from two areas as indices of

the relative population strengths of those areas it can be found whether the black phase is more frequent in areas more densely populated by possums. Taking the thirty stations in the North-Western area of high percentage of melanics as an example and comparing it with the fifty-three stations in the Midland area with a high percentage of the grey phase, it is found that the average return per station in the North-west area is 120.6 skins, whereas in the midland region there are 659.6 skins returned per station. This indicates that the melanics are not plentiful in areas of greater population density which is the reverse of Gerschenson's conclusion (1945a), relating to hamsters. The effort of hunting is more concentrated in the North-western area (297 licences) than in the Midlands (97 licences) which means that the yield per station should be higher if the population were greater. This is not the case.

Relation of distribution to topography

Examination of the topographical map (Fig. 2) shows that there is no correlation between the distribution of the two colour phases of *Trichosurus* and the main topographical features of the country. The midland-eastern region of high percentage of grey possums extends from high country to coastal areas and the Western area also contains much high land as well as some low-lying areas. Pearson (1938) also failed to find any correlation with topographical features.

Relation of the distribution to climate

Figure 3 shows the climate of Tasmania as classified according to Thornthwaite (1931). This figure is taken from a map in the Regional Planning Atlas for Tasmania.

FIG. 2. The topography of Tasmania.

FIG. 3. The climate of Tasmania, based on Thornthwaite's classification. (Modified from the Tasmanian Regional Survey Atlas).

The regions with a high percentage of the melanistic variety are found in areas of superhumid and humid conditions, but this correlation is not very close and it breaks down in the Buckland-Nugent Pocket, where there is a belt of high percentage blacks running across South-eastern Tasmania to the East coast. In this Pocket, black possums are numerous in areas classed as dry humid. The correlation in the North-east area is not very close but this might fall within the limits of experimental error allowing for the method of recording locality data.

The Midland-eastern region extends from the warmest and least humid part of Tasmania to the coldest most humid region, and it is not possible to find any relationship between the presence of the grey phase and the nature of the climate. The climate has little direct effect on the distribution of the possums except in that it controls the vegetation.

Relation of the distribution to rainfall

The rainfall in Tasmania is shown on Figure 4, which is based on the map published by the Weather Bureau (1936). The correlation of the phenocontours with the rainfall is fairly good though, as will be seen below, it breaks down in certain regions.

The North-western, Western and Southern possum regions all fall into the western area of Tasmania which experiences a heavy rainfall of more than 40". Some parts of the Nugent-Buckland Pocket experience a 30" rainfall. The north-eastern possum area also occurs in an area of more than 40" rainfall and the Midland-eastern area is in a low rainfall belt. Table III shows the possum areas and the correlation with rainfall.

From the above table it can be stated in general

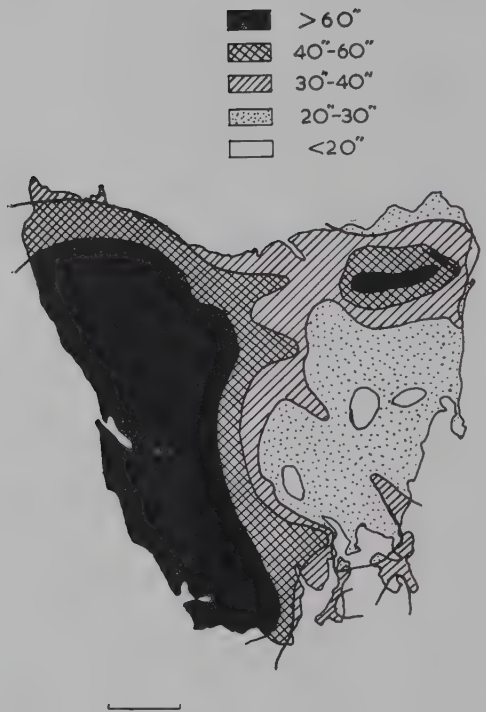

FIG. 4. The rainfall in Tasmania. (Based on a map published by the Weather Bureau, 1936.)

TABLE III. Possum distribution areas and rainfall.

Possum area	Rainfall	Percentage Blacks
North western	40"	75–100
Northern	20" - 40"	50
North eastern (Blue Tier)	40"	60– 85
Western	40"	75–100
Southern less the "Pocket"	40"	100
Buckland-Nugent	20" - 40"	100
Midland-eastern	30" - 40"	0–25
Flinders & King Is.	20" - 30"	0

terms that areas populated by over 75% of black possums have more than 40" rainfall. A region with less than 30" rainfall supports between 50 and 100% grey possums. Areas of 30"-40" rainfall support a very mixed possum population.

Areas where the rainfall correlation is not good are Lake Margaret, rainfall 120" with 100% grey possums, West of Lake St. Clair, over 80" rainfall but with a high percentage of grey possums, and the Buckland-Nugent Pocket.

Relation of the distribution to forest area

Wet sclerophyll forest areas in Tasmania are usually found in regions with above 40" annual rainfall. However, in some gullies which are sheltered from strong sunlight, a rainfall of 30" is sufficient to produce sclerophyll forest.

In regions where the rainfall is above 60" per annum the wet sclerophyll forest is replaced by *Nothofagus* (Myrtle) forest.

There are many exceptions to these general rules, for example at Lake St. Clair where the rainfall is over 80" the myrtle forest does not develop due to excessive soil drainage.

The dominant trees of a wet sclerophyll forest are three species of the genus *Eucalyptus,* namely *obliqua, gigantea* and *regnans* with an understorey consisting of *Bedfordia salicina, Atherosperma moschata* (sassafras), *Olearia argophylla* (Musk) *Pomaderis apetala* (Dogwood), *Plagianthus sidoides, Acacia verniciflora, Dicksonia antarctica* (Tree Fern), *Plebalium billardieri* (Lancewood), *Gahnia psittacorum* (cutting grass), and the woody climbers *Lysonia strominia* and *Clematis aristata.*

The resulting forest is very thickly colonized by plants and leads to humid conditions as is shown by the presence of epiphytes on *Dicksonia,* for example *Tmesipteris* and *Hymenophyllum* spp.

Myrtle forests, on the other hand, consist of pure stands of *Nothofagus cunninghami*—often without an understorey. The substratum is often covered by mosses and does not support any other small plants. The myrtle forest is also very wet and humid but differs considerably from the *Eucalyptus* forest in that it does not appear to support many marsupials. This statement cannot be verified by any of the figures derived from the royalty returns, but Mr. Gilbert of the Forestry Commission has never seen kangaroos or possums in myrtle forest areas and other reports support his observations though wallabies are found in clearings in thick myrtle forest.

The map showing the isohyets in Tasmania also serves to show the distribution of forests, though small areas of button grass, *Gymnoschoenus sphaerocephalus* are shown as forest. In the East Coast area, there are many gullies which contain wet sclerophyll forest although the rainfall is less than 40" per annum.

As noted above, the distribution of the black colour phase of *Trichosurus* closely follows the 40" isohyet except in the certain areas. These areas are:

Lake Margaret	120" rainfall—100% grey.
West of Lake St. Clair	80" rainfall— 60% grey.
Buckland Nugent Pocket	30" rainfall—100% black.

In the region lying to the west of Lake St. Clair we find that the forest is not well developed, being of an open savannah nature with large areas of

button grass plains. This type of country extends for some distance towards the West Coast.

Around Lake Margaret there are few trees, though there is very thick sclerophyll forest in adjoining gullies.

On the west coast there is a region of moderate percentage melanics which extends for some distance inland. There is not much evidence for the inclusion of this belt (Station 122, sample strength 20) but when the little available evidence is considered in conjunction with the local vegetation, which is either button grass or dense myrtle forest, there is some justification for the inclusion of this area.

In the North-eastern region, the area of dense forest shows a high percentage of black possums, but in the South-east on the Forestier Peninsula and the Tasman Peninsula there is a low percentage of blacks. This may be largely due to there being little hunting carried on in this area. During the 1949 and 1952 open seasons no licences permitting either hunting or the sale of skins were issued on either Peninsula. Such a small amount of hunting will, of course, lead to poor sampling of the population with consequent incorrect results. It seems probable both on the type of forest and the rainfall encountered, that the South-eastern region has a greater percentage of melanics than is shown by the available figures.

The Buckland-Nugent Pocket

This pocket of high percentage of melanics does not show an immediately apparent correlation with any of the facts considered above. However, a more detailed examination of the data from each of the stations in the area produces certain interesting facts.

Station 218 Pelham. Sample strength 1. This sample is too small to be of any significance.

Station 169 Gretna. Sample strength 40. Percentage black—100.

Station 57 Broadmarsh. Sample strength 26. Percentage black—100.

These two stations are situated in close proximity to Mt. Dromedary (3245′) which is an area with a *Eucalyptus regnans* forest, that is wet sclerophyll forest.

Station 180 Dysart. Sample strength 27. Percentage black—100.

Station 102 Colebrook. Sample strength 25. Percentage black—100.

The country around Dysart and Colebrook is all timbered and in some places the timber is thick. Mt. Quoin, 2950′, lies a short distance to the North-east of Dysart. The mountain is thickly timbered.

Station 104 Buckland. Sample strength 29. Percentage black—100.

Station 106 Nugent. Sample strength 11. Percentage black—82.

These two stations lie in a region which is characterized by a solid belt of thick forest, although the land in the area is not as high as around Dysart.

The phenocontours defining the Buckland-Nugent Pocket are shown in Figure 1 as a continuous line running from Dysart to the coast and returning a few miles to the south of Collinsvale (Station No. 38). There are no stations giving data between Colebrook and Buckland but in this area there is very little timber of any sort and certainly no thick forest. It seems more likely that the curve should be as shown in Figure 5 where the areas are shown as separate regions.

FIG. 5. The Buckland-Nugent pocket, showing the probable distribution of the black phase.

EFFECT OF FOREST CLEARANCE ON POPULATION COLOUR

Dr. J. Huxley suggested that it would be interesting to check if areas where forest clearance had taken place showed any abnormal proportion of black possums. Considerable clearance has taken place in all of the northern area. This area, now about 50% black possums, may at present be in a state of change, though it has been suggested above that the distribution of forest is the probable reason for the mixed population.

At Parrawe (St. 183) and Highclere (St. 185) considerable clearing has taken place but the percentage of black possums is still high, which is in accordance with expectations in that area. However, other stations (Queenstown St. 122) and St. 8 (53% grey): Lune River, St. 24 (17% grey); Oonah, St. 28 (67% grey) and Waratah, St. 36 (9% grey) show abnormally high proportions of grey possums. Usually where forest clearance takes place, the devastation is fairly complete and the area becomes unsuitable for trapping and returns are not made from such centres. Around Parrawe and Highclere there are no trees at all

but the animals on which the return is based come from nearby rainforest. As a result of mining operations greater timber clearance has occurred around Queenstown and Waratah and at these places the population of blacks is unusually low, especially at Queenstown (67% and 15%) where great devastation has been caused by sulphurous fumes. At the Lune River and Oonah the clearance is due to logging operations.

If some selective factor is at work it might be expected that in areas cleared of forest, the percentage of black possums would be lower than usual. There is a slight indication that this might be so but it is not possible to check this with accuracy.

Alteration in the Phenocontours since 1938

It was also suggested to us by Dr. Huxley that it would be interesting to treat our new data by the same method at that used by Pearson, namely to take similar areas to those established by Pearson and aggregate the samples for those areas.

As far as possible our stations are the same as Pearson's though in some cases there may be a larger area in the same stations.

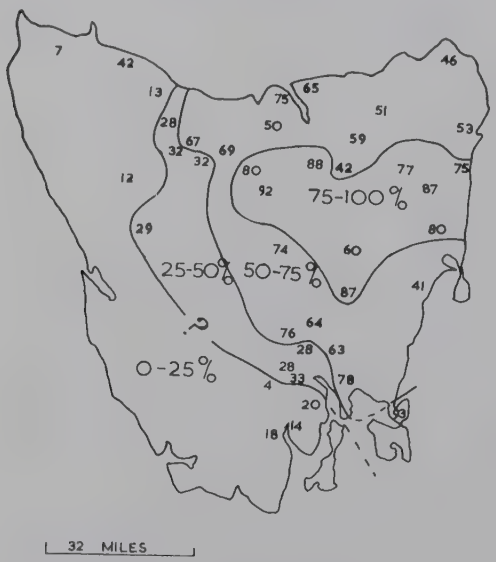

Fig. 6. The present distribution of *Trichosurus*, following the method used by Pearson (1938).

These results when graphed (Fig. 6) give a series of phenocontours which are significantly close to those derived by Pearson. The greatest difference in the two figures lies on the West Coast where the region of high percentage melanics has moved further to the East. (Compare Fig. 6 with Fig. 7.) The area of high percentage greys appears to have moved further to the North. The important feature is that the form of the phenocontours is the same in both figures and the differences noted above are probably due to methods of sampling and treatment of the results.

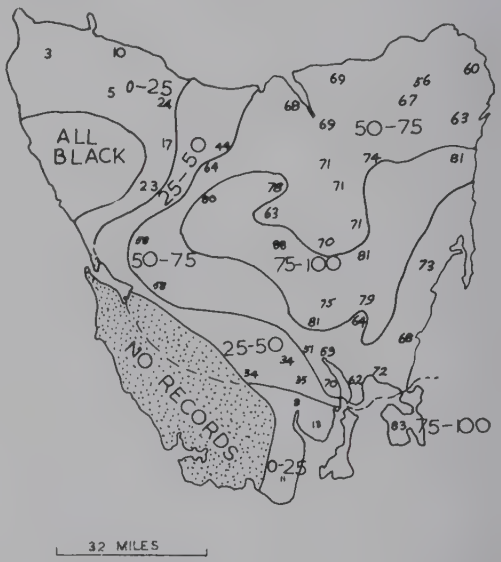

Fig. 7. The distribution of *Trichosurus* in 1937, after Pearson (1938).

Five of Pearson's stations are not plotted on Figure 6 as we have no records from these localities. However, comparison between Figure 1 and Pearson's table shows that these stations fall within the appropriate percentage groups. Twenty-six of our stations could not be grouped satisfactorily into any of Pearson's areas.

Discussion

According to Iredale and Troughton (1934) there are several different subspecies. They are *T. v. vulpecula* Kerr, found in New South Wales, Victoria, South Australia and S. Queensland, *T. v. fuliginosus* Ogilby occurring in Tasmania and 6 other subspecies of restricted range. The subspecies *fuliginosus* has been suggested by Troughton (1941) to be a separate species, *T. fuliginosus*, but this has not been followed by other workers. The Tasmanian subspecies is larger, with a stronger skull and probably bears a larger and more dense coat than the Mainland subspecies. It is significant that the New Zealand workers recognise only *T. vulpecula*, although the possums introduced into the country came from both Victoria and Tasmania and were therefore both of the subspecies *T. v. fuliginosus* and *T. v. vulpecula*.

Although it is clear that *Trichosurus* occurs on the mainland of Australia in several subspecies based on colour differences, it is far from clear as to the types of country in which the different subspecies are found, nor is it known whether the subspecies are found living together with other colour forms. However, it is apparent that grey is the common colour of the species. Dunnet (1956) does not record black possums in the Canberra area which might be expected from the dry nature of the country. If there were any differentiation of colour phases due to habitat influences on the Mainland it seems unlikely that it would not have been recorded in the literature. It is significant in this regard that the related *T. caninus* Ogilby from New South Wales has been recorded with a subspecies *T. c. nigrans* Le Soeuf found in heavy coastal scrub, *i.e.* a humid habitat.

Tasmania and Australia were at one time connected by a land bridge extending across Bass Strait from S. W. Victoria via the Furneaux Group of islands to N. E. Tasmania. The probable route of migration of the possum was from Victoria across this bridge over Flinders Island and into N. E. Tasmania. Acceptance of this fact makes the Australian and Tasmanian possums genetically homologous at the time of invasion. The bridge was submerged as a result of the melting of the Pleistocene ice sheets some 25,000 years ago. Thus the presumed point of entry of the possum into Tasmania is in a region of high percentage grey colour but it is also in a region of dry light scrub covered country. Flinders Island, with 100% grey possums, possesses similar country. In this we agree with Pearson. As the possum spread across Tasmania the black phases appeared as mutations from time to time and, by chance, found themselves in a region ecologically suited to them, namely high rainfall and heavily timbered country, with a minimum of diurnal temperature variation. This type of country conferred some selective advantage upon the blacks and they gradually became the dominant phase in that type of country.

Barber (1954) has shown that the black color phase of the rabbit, *Oryctolagus cuniculus* (L.) closely follows the distribution of the black possum.

The possum follows Gloger's Rule that the more melanic phases of a species are encountered in more humid regions. There are no intergrades from melanic to grey phase. Indeed, in many places black and grey possums occur together and they are known to breed together. However, in the case of the possum the cline is very steep, stations a few miles apart showing a change from 100% of one phenotype to 75% of the other.

It remains to discuss the selective advantage which the black possums obtain in humid habitats. There is little or no predation upon this species. Being nocturnal, it is protected from attacks by eagles, though owls may take young animals. We have found *Trichosurus* fur in scats of the Tasmanian Devil, *Sarcophilus harrisii* (Boitard). It is by no means certain that the Devils prey upon *Trichosurus,* though they can climb trees. It is probable that the *Trichosurus* had been eaten as carrion.

Barber (1956) asks some pertinent questions about the selective advantage of the black rabbit in certain types of country. Two of those questions can be asked in relation to the distribution of the black possum. Is there protection against predators to be gained by being black in humid forested areas or conversely, a disadvantage in being black in more open areas? We doubt if there is because of the nocturnal habit of the species and an apparent absence of suitable predators. The second question is physiological in nature, namely can heat radiation place a greater strain on the black in the regions of greatest temperature change, *i.e.* open savannah type country? Black animals will lose heat by radiation more readily than grey coloured species. These questions are yet unanswered.

It is interesting to note that the Brush Possum was introduced into New Zealand, several introductions being made at different places and different times (Pracy and Kean 1949; Wodzicki 1950). The stock was derived from both Victoria and Tasmania but there has not yet been any comparable segregation of the two colour phases into a distribution pattern. Kean (personal communication) considers that the dominant factor governing the distribution of the colour phases of *Trichosurus* in New Zealand is still the colour of the original stock at the point of introduction.

It was shown by Pearson (1938) that there was no correlation between the distribution of the black and grey colour phases of *Trichosurus vulpecula* and the topography of Tasmania. With this result we are fully in agreement. Where Pearson plotted his phenocontours on 47 stations we have utilized 242 and this has enabled us to draw a more detailed picture of the distribution of the colour phases of this species. In particular, the region of high percentage melanics in the North-east corner of the State and in the Buckland-Nugent Pocket show changes from the distribution as found by Pearson. It is noteworthy that Pearson also found a high percentage of greys extending over towards the West Coast far beyond the 40" isohyet, which accords with our own findings. The all-black area in the North-

west shown in Pearson's map, based on trappers' evidence, was not supported by evidence from at least one station of the present survey.

We find that the climate (as classified by Thornthwaite) does not have a direct correlation with the distribution of the black phase of *Trichosurus,* though it almost certainly has an important secondary influence. The principal factors affecting the distribution of the black and grey colour phases are rainfall and vegetation. The black phase is found in areas of thick sclerophyll forest with an annual rainfall greater than 40". Areas with more than 40" of rainfall but without a sclerophyll forest have a high percentage of grey possums. On the North coast where there is a large area showing very mixed samples, it is probable that the methods used are not sufficiently detailed to pick up the microdistribution of the species in a region of very mixed vegetation.

We agree with Pearson that since the possum belonged to the once geographically continuous race when it arrived in Tasmania, it was genetically homologous with the Mainland race. In other words, melanics appeared sporadically in both Tasmania and Australia. However, as the species spread in Tasmania it encountered regions with very humid conditions and these apparently conferred some selective advantage on the black phase which has become numerically dominant in those areas. It is significant that Le Souef (1916) recorded the melanics as numerous in rainforest in South-western Australia. The grey phase is most frequent in areas of lower humidity, *i.e.* the islands of Bass Strait, the mainland of Australia and certain parts of Tasmania.

Gerschenson (1945a) found that the black phase of *Cricetus* lives in similar situations and that in common with other melanics this phase is genetically dominant. It is probable that the melanism is also dominant in *Trichosurus* and that this dominance confers some selective advantage in humid situations where melanics are more frequent in occurrence.

Summary

1. The distribution of the black and grey colour phases of *Trichosurus vulpecula* (Kerr) is obtained from fur industry returns.

2. Tasmania can be divided into seven possum distribution regions based on the percentage occurrence of the colour phases.

3. In general, the transitional regions between areas of high frequency colour phases are very narrow. This may be obscured by the microdistribution of the colour phases which cannot be detected by the methods used.

4. It is found that there is no correlation between the distribution and topography but that there is a secondary relationship with climate.

5. The principal factors influencing the distribution are vegetation and rainfall. The black phase favours wet sclerophyll forests with over 40" annual rainfall while the grey favours more open forests with more or less than 40" precipitation.

6. It is possible that forest clearance results in a higher proportion of grey possums being found in cleared areas. This cannot accurately be verified by the present methods.

7. Our data, when treated according to Pearsons' method, show that little significant change has taken place in the distribution pattern since 1938.

Acknowledgments

We are indebted to Mr. Shirley of the Police Department for access to the duplicate royalty receipts and to Mr. M. Gilbert, B.For., who gave us valuable information regarding the distribution of forests in Tasmania; Mr. Angus Love of the Lands and Surveys Department assisted us in locating some of the stations. To Dr. Winifred M. Curtis of the Botany Department of the University of Tasmania we are indebted for information on the composition of sclerophyll forests and to Dr. J. S. Huxley who gave us valuable suggestions which were incorporated in the above. Mr. Peter Scott, M.Sc.(Econ.) of the Geography Department of the University of Tasmania suggested the use of proportional circles in the distribution map. Professor V. V. Hickman very kindly checked the typescript and suggested many improvements. Dr. Ralph W. Dexter, Kent State University, Kent, Ohio, saw the manuscript through the press.

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PLEISTOCENE GEOGRAPHY AND THE DISTRIBUTION OF NORTHERN PINNIPEDS

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The history of land mammals during the Pleistocene has received attention from many authors on many occasions, but attempts at interpreting the significance of Pleistocene events in their relation to the distribution and differentiation of marine mammals seem to have been notably absent. The general reluctance to discuss the distributional history of marine mammals is connected with the relative absence of fossil remains and the supposition that the various forms are pelagic and that, therefore, lines of population migration, expansion and contraction are less easy to reconstruct. But the pinnipeds with few exceptions are not totally pelagic and, in the case of those exceptions, their distributions and movements are closely tied to those of sea ice. Existing species show well-marked ecological preferences and the geographical distribution of many is limited and not difficult to define. I believe that it is possible, without indulging in excessive hypothesis, to draw conclusions about the past history of many species and, in particular, those inhabiting the Arctic basin and the contiguous parts of the North Atlantic and North Pacific Oceans.

No attempt has been made to document completely all the evidence discussed. The greater part of it is well known and, I believe, generally accepted by workers in the fields of Pleistocene geology and pinniped biology. The present study represents an attempt at a partial synthesis of the two fields. Where I have been somewhat controversial, as in the discussion of the relationship between *Phoca groenlandica* and *Phoca fasciata*, fuller documentation is given. Full bibliographies are given in some of the works cited, especially Flint (1947) for Pleistocene geology and Deevey (1949) for Pleistocene biogeography in the northern hemisphere. The most extensive bibliography of works on northern seals is probably that in Mohr (1952).

I am indebted to Prof. H. N. Barber and Prof. K. E. Caster for reading and commenting upon the manuscript.

The Northern Pinnipeds

The species dealt with in the present discussion comprise all the family Odobenidae and, within the family Phocidae, all the Phocinae and the genus *Cystophora* of the Cystophorinae. The remaining Phocidae are of tropical and southern distribution. The third family, that of the Otariidae, is representd in the boreal Pacific by *Eumetopias jubata* and *Callorhinus ursinus* and in the warm temperate Pacific by *Zalophus californianus*.

Nomenclature follows Ellerman and Morrison-Scott (1951) and Miller and Kellog (1955), except that I have followed Sivertsen (1954) in regarding the Japanese sea lion as synonymous with *Zalophus californianus*. The forms referred to are listed below.

Family OTARIIDAE
  Subfamily ARCTOCEPHALINAE
    Callorhinus ursinus, northern fur seal; subspecies *ursinus, cynocephalus, curilensis*.
  Subfamily OTARIINAE
    Eumetopias jubata, northern sea lion.
    Zalophus californianus, California sea lion.
Family ODOBENIDAE
    Odobenus rosmarus, walrus; subspecies *rosmarus, divergens*.
Family PHOCIDAE
  Subfamily PHOCINAE

Phoca vitulina, harbour seal; subspecies *vitulina, concolor, mellonae, richardii, largha, geronimensis.*
Phoca hispida, ringed seal; subspecies *hispida, botnica, ochotensis, saimensis, ladogensis, pomororum, birulai, kraschenini-kovi, beaufortiana, soperi.*
Phoca caspica, Caspian seal.
Phoca sibirica, Baikal seal.
Phoca groenlandica, harp seal; subspecies *groenlandica, oceanica.*
Phoca fasciata, ribbon seal.
Erignathus barbatus, bearded seal; subspecies *barbatus, nauticus.*
Halichoerus grypus, grey seal.
Subfamily CYSTOPHORINAE
Cystophora cristata, hooded seal.

Because of the great individual variation in cranial characters, particularly with sex and age, taxonomists have found the pinnipeds a difficult group. It is clear that a large series of specimens from any given population is necessary before valid conclusions can be drawn and a very large number of synonyms has arisen because this necessity has not been sufficiently appreciated. In the case of the forms listed above, I believe that a sufficient degree of stability in the taxonomy has now been reached to warrant their acceptance as a basis for discussion. It would not be surprising if some of the named races of *Phoca vitulina* and *Phoca hispida* proved to be not significantly differentiated, but it is unlikely that revision of these species would considerably affect the arguments which it is proposed to advance.

The fossil record in respect of these forms and their possible ancestors is very meagre. It is of small value in delineating past distributions, which must generally be inferred from the limitations imposed by Pleistocene geography. That these limitations were considerable and capable of reasonable reconstruction is largely the thesis of the present paper.

The maps of modern distribution are based principally upon Bobrinskii and others (1944), Dunbar (1949) and Anderson (1946), although numerous other authorities have been consulted in an endeavour to make them as precise as is at present possible. A problem which arises in the mapping of seal distributions is that there is nearly always a significant difference between the total range of a species and its effective range. Occasionally, individuals will appear in localities far from their normal habitat in a way that is not paralleled in land mammals. Records of such occurrences have tended to obscure the effective range of the species concerned, because authors have often repeated the records without due regard to their true significance. In the maps accompanying the present discussion, I have attempted to show what appears to me to be the effective range of each species.

The Geography of the Pleistocene Arctic

Pleistocene events are conveniently and authoritatively summarised by Flint (1947). Since the genus *Phoca,* at least, has been found in the Miocene of Europe and the Pliocene of eastern North America, there is evidence that some of the forms under consideration, or their ancestors, have been present in northern waters since before the Pleistocene. Among existing species, *P. groenlandica, P. vitulina, P. hispida* and *Erignathus* are recorded from the Pleistocene, (Kellogg 1922). They must consequently have been subjected to the spectacular and relatively rapid climatic and geomorphic changes which occurred during that epoch. Broadly speaking, there were four major times of formation and expansion of ice sheets separated by three interglacials when the climate was a little warmer than at present. During each glacial age, the ice sheets reached a roughly similar limit, but, in Asia at least, the third was more extensive. In each interglacial, temperatures appear to have been comparable, although the second interglacial was significantly longer than the other two. At present about ten per cent of the land area of the world is covered by ice sheets as compared with about thirty per cent during glacials, so that conditions are now intermediate between those of glacial and interglacial times.

A second important feature of Pleistocene geography was the rise and fall of sea level resulting from the alternate capture and release by the ice sheets of part of the world's water resource. Although no reliable quantitative assessment of this can be made, its importance from the point of view of the present discussion is that the fall in sea level during at least one, and possibly all, glacials must have been sufficient to extinguish the Bering Strait and give rise to an effective barrier between the Arctic Ocean and the North Pacific. Evidence provided by the migration of land mammals between Siberia and North America suggests that the barrier existed almost continually in the early and Middle Pleistocene (Simpson 1947).

Although some information is available as a result of the examination of sea-floor deposits, marine conditions during glacial and interglacial periods must largely be inferred by arguing from the distribution of sea ice in relation to air temperatures and glaciers as they exist today to air temperatures and glaciers as they have been reconstructed for various sections of Pleistocene

time. Figure 1 indicates present conditions. In the centre of the Arctic basin is a zone of more or less permanent sea ice—the so called "permanent pack." With the possible exception of the ringed seal, *Phoca hispida,* which has been recorded in small, temporary, open leads, pinnipeds do not exist within this area and its edge constitutes the northern limit of distribution for all the more northern species. Surrounding this is a zone in which surface ice forms and disappears seasonally, the exact period of disappearance varying from place to place, but being generally much shorter towards the edge of the permanent pack

FIG. 1. The Arctic region at present. Glacial ice \\\\\\\ ; edge of permanent pack ------- ; edge of seasonal pack — — — .

This is here called for convenience the "seasonal pack" and its average extent in each month of the year can be obtained by reference to the Ice Atlas of the Northern Hemisphere (U. S. Hydrographic Office 1946). The distribution of the seasonal pack is closely related to the location of warm and cold sea currents and it extends much further south in the west Atlantic and west Pacific than it does on the east side of those two oceans.

Figure 2 attempts to show conditions as they existed in the fourth glacial, or, approximately, during any of the glacial ages. It is based primarily on Flint (1947) with the addition of probable contemporary shorelines and an estimate of the extent of the permanent pack. The seasonal pack, as shown by Flint, has also been extended to include the Sea of Okhotsk. Flint's map shows no ice here at all, although there is extensive ice formation today and the ice would certainly have reached the Kuriles at its annual maximum in

FIG. 2. The Arctic region in the fourth glacial but with Siberian glaciers as in the third glacial. Glacial and sea ice shown as in Fig. 1 (mainly after Flint 1947).

glacial ages. At such times the whole of the Arctic basin would have been covered by the permanent pack and largely fringed by glacial ice. It was cut off from the Pacific either by a land bridge across Bering Strait or by permanent ice forming in very shallow water. Towards the Atlantic, the permanent pack must have extended at least as far as is shown in Figure 2 and may also have filled what is now Baffin Bay. Seasonal pack filled the Bering Sea and the Sea of Okhotsk and probably extended from Newfoundland to Britain, well to the south of its existing range. Where glacier ice reached the sea, as along the American coast between Long Island and Newfoundland, there would have been great cliffs of shelf ice similar to those in the Ross Sea of Antarctica today.

It must be admitted that ice conditions during interglacials are much more difficult to assess and whether or not sea ice completely disappeared during such times is not known. However, it must have been considerably less extensive than at present and it is probable that there was free water between the Pacific and the Atlantic at all times of the year. If we may judge by the way in which the pack has been receding with the slight increase in temperature during the last few decades, sea ice is particularly sensitive to changes in atmospheric temperatures and there must have been small but significant variations in its extent since the initial recession of the last ice sheets. The thermal maximum of about four thousand years ago must have caused a particularly well marked decrease in pack ice, although not as much,

nor for anything like as long a period, as during the interglacial ages. It is unlikely that there has been any well marked recession of range of species since the thermal maximum, except possibly in the case of *Phoca vitulina*. *Odobenus* and *Erignathus* have not yet fully reoccupied areas which seem well suited to their requirements.

Whatever uncertainties may exist regarding the exact extent of sea ice during glacial and interglacial ages, it is difficult, if not impossible, to avoid the conclusion that the Arctic basin must have been uninhabitable for seals during glacials (with the possible exception of *Phoca hispida*) and much more habitable than at present during interglacials.

Present Ecology of the Species

Before attempting to proceed further with the argument, it is necessary to examine the ecological niche occupied by each of the species at present living in northern waters. This is probably most readily understood by reference first to relationships with ice and second to feeding habits, although the two are to some extent interconnected.

The most northerly species of all is *Phoca hispida,* the range of which may extend into the permanent pack and which is the only truly circumpolar pinniped in the sense that its range extends uninterruptedly around the Arctic Ocean. The bearded seal, *Erignathus,* is also an inhabitant of this most northerly zone and extends almost as far north as *hispida* but is tied to coastal waters by its feeding habits. These are the two species which are able to keep open breathing holes in the ice and are very closely connected with the pack at all times of year. More southerly in distribution is the walrus, *Odobenus,* which, both in the Atlantic and Pacific appears generally to migrate north and south with the pack ice edge. The next three species, *Phoca groenlandica, Phoca fasciata* and *Cystophora cristata,* are more southerly still in distribution and are very closely tied to the ice edge. They breed in early spring on the pack at its most southerly extension and undertake pronounced seasonal movements northward as the ice recedes, but do not regularly move as far north as the first three species mentioned. The grey seal, *Halichoerus,* and *Phoca vitulina* are boreal in distribution and are rarely associated with ice. *Halichoerus* does, however, breed on the early spring ice of the Baltic and the Gulf of St. Lawrence and *P. vitulina* regularly moves a considerable distance north during the summer months, especially in the east Canadian Arctic. The Otariidae species are all boreal and warm temperate in distribution and normally have no contact with ice.

It is possible then to arrange the northern pinnipeds into four groups according to their relationship to sea ice and sea temperatures, and the species occurring within these zones differ in their feeding habits. In the more northerly zone of the seasonal pack (here called "arctic"), *P. hispida* is small, largely pelagic and a plankton eater, while *Erignathus* is a large animal of the coast, feeding on benthonic invertebrates. In the more southerly zone ("subarctic" here), *Odobenus* is a very large animal almost always closely tied to the shore and feeding, like *Erignathus,* primarily on bottom invertebrates. *P. groenlandica* and *Cystophora,* on the other hand, are both pelagic, breeding on the ice many miles from land, but differing in their feeding habits in that *groenlandica* takes a large proportion of planktonic crustacea while *Cystophora* is a larger species with a diet in which fish play a more important part. Likewise, in the boreal zone, *P. vitulina* is smaller and not so predominantly a fish eater as is *Halichoerus* and the two species tend to occupy different types of coasts. In the Pacific, *Callorhinus,* although breeding in the Bering Sea, does almost all its feeding on seasonal migrations southward into the boreal zone, where it is pelagic. It feeds on fish and large invetebrates, as does *Eumetopias,* which is also boreal but is a larger animal and much more coastal in feeding habitat. *Zalophus* is warm temperate in distribution and does not overlap the range of the other two Otariids, except in parts of California and Japan.

These ecological relationships are summarised in Table I. It will be appreciated that the remarks made here on ecology are essentially generalisations and in practice there is overlapping in range and in feeding habits, but this should not materially invalidate the broad picture as here set out. I use the terms "arctic," "subarctic," "bo-

Table I. Generalized ecological relationships of northern pinnipeds

		Size: large Food: bottom invertebrates	Size: medium & small Food: plankton & fish	Size: large Food: fish
Atlantic	Arctic	*Erignathus*	*Phoca hispida*	....
	Subarctic	*Odobenus*	*Phoca groenlandica*	*Cystophora*
	Boreal	.....	*Phoca vitulina*	*Halichoerus*
Pacific	Arctic	*Erignathus*	*Phoca hispida*	.....
	Subarctic	*Odobenus*	*Phoca fasciata*	.....
	Boreal	.....	*Phoca vitulina*	*Eumetopias*
	Warm Temp.	.....	.....	*Zalophus*

Note: *Callorhinus* would fit into this scheme with *Eumetopias*, but is smaller, migratory and pelagic outside the breeding season, whereas the latter species is larger, sedentary and coastal in distribution.

real" and "warm temperate" with some hesitation and in the broadest possible sense.

Past Ecology of the Species

If we could assume that the ecological niche occupied by each species has remained the same through at least two glacials, the task of reconstructing past distributions would be much simplified. Whereas existing genera may be traced back in the fossil record well into the Tertiary, existing species cannot be identified earlier than the Pleistocene. They have evolved in an epoch when there have been spectacular changes in the distribution and extent of sea ice and it is reasonable to suppose that ice relationships and even sea-temperature relationships would vary with these changes. During glacials when ice habitats were at a maximum there would be a tendency towards increasing adaptation to ice. During interglacials, when warm water habitats were at a maximum, there would be a tendency towards adaptation to free water. This process can be seen in operation today, for in both the boreal species, *P. vitulina* and *Halichoerus grypus,* there is a very much more marked tendency for the population groups in the colder western parts of the Atlantic to come in contact with and adapt themselves to ice than there is on the part of the eastern groups in the same ocean. Thus *Halichoerus* in the east Atlantic does not normally come into contact with ice and its range is bounded to the north by the southern limit of the seasonal pack, but the group in the west Atlantic has adapted itself to life in the Gulf of St. Lawrence where it breeds on the ice and has even changed its breeding season. The *concolor* race of *vitulina* in the west Atlantic moves far north into the subarctic zone and has even been reported from Ellesmere Island. According to Doutt (1942), it breeds in Hudson Bay and has produced a landlocked freshwater form in an Ungava lake. The *P. vitulina* of Europe, in contrast, rarely if ever moves into the zone of the seasonal pack. Similarly, in the Pacific, Wilke (1954) records a population of *vitulina* which breeds on the ice in the Okhotsk Sea and has, like the Canadian *Halichoerus* population, changed its breeding season, whereas the *richardii* race of the east Pacific has no normal contact with ice. There it little doubt that this marked tendency on the part of both *P. vitulina* and *Halichoerus* results from the greater amount of ice in the western parts of the two oceans and can be taken as a guide to the probable reaction of all species to the expansion and contraction of sea ice during the Pleistocene.

A second tendency which it is necessary to bear in mind is that a telescoping of the total range would have occurred during glacials, so that the distance from the most northerly specimen of *P. hispida* to the most southerly specimen of *P. vitulina* must have been less than it is today or was during interglacials. This is graphically illustrated by the rapidity with which the arctic *P. hispida,* the subarctic *P. groenlandica* and the boreal *Halichoerus* followed each other into the Yoldia Sea of Scandinavia, which may have lasted only a few hundred years (see species discussions below).

But, while bearing these two tendencies in mind, I believe that the space relationships of the various species have remained generally constant for a very long time. My reasons for believing this are that not only is it strongly suggested by the conclusions reached in the present study, but it has also been an important factor in speciation. This is especially the case in the genus *Phoca,* where, in the North Atlantic, the three species are kept apart by the differences in their relationship to ice (see Table I).

Feeding habits have almost certainly remained more stable than have ice relationships and are in some ways a more reliable guide to probable past distributions. The most convincing evidence which can be offered in support of this assertion is probably that of the dentition of the various species. It is becoming increasingly evident that the character of the teeth in each species is closely related to the diet and this can readily be illustrated from Table I. The two species feeding on bottom invertebrates have aberrant dentition. In *Odobenus* the extraordinarily elongated upper canines seem to be used for grubbing in the mud and sand of the bottom, for many of the molluscs on which it feeds live buried. By contrast, *Erignathus* seems to be in process of losing its teeth completely. Allen (1880) describes them as "small, molars spaced, slightly implanted, early becoming defective by attrition; partly deciduous in old age." The *Phoca* species, with the exception of *fasciata,* feed primarily on planktonic and other invertebrates and have molars with three or four cusps, while *Cystophora, Halichoerus* and the Otariids are primarily fish eaters and have relatively simple, almost conical molars. So strong is this connection between dentition and feeding habits that it is difficult to believe that the latter have not been generally stable at least since the third glacial, or about 300,000 years, which is all that is required for the present argument.

It is concluded, therefore, that the nature of southward and northward movements during the late Pleistocene at least, would be controlled by feeding habits which would be generally static, and by sea temperatures and relationship to ice, which would tend to vary more between glacial

and interglacial ages, although the relative distribution of the various species probably remained the same.

That species moved south of their present range during glacials is attested by fossil finds: for example, Kellogg (1922) mentions Pleistocene remains of *Odobenus* (= *Odobenotherium*) and *P. groenlandica* in eastern North America well south of where they are found today and *P. groenlandica* in south-western France. That species moved north of their present range in interglacials is proved by the presence on both Atlantic and Pacific sides of the Arctic basin of subspecies so barely distinguishable that they cannot have become differentiated before the Middle Pleistocene. The only way in which such southerly species as *P. vitulina* could have spread from one side of the Arctic to the other is by a considerable northward extension of range in an interglacial period.

The Effect of Repeated Movement

Before proceeding to a discussion of individual species, one more general observation should be made. It will be argued that the expansion and contraction of glacial and marine ice during the Pleistocene was instrumental in determining the present distribution of species and in giving rise to existing geographical subspecies. This was accomplished by separating Pacific from Atlantic populations, by separating populations on either side of those two oceans and by cutting off small population groups in lakes and semi-isolated seas. This process of separation must have operated in each of the four glacials, but the fourth and, in some instances perhaps, the third has effectively created the present pattern. If population groups were isolated by the expansion of ice sheets in the first three glacials, then there was opportunity for resumed gene flow between those groups when they came into contact once more during the interglacial ages. In the same way, if ice retreat continues today, many existing geographical races will meet and interbreed so that there will be a merging of stocks. Succeeding glacials would tend to repeat the same process, so that if the last was not initially responsible for present conditions it must have emphasised the effects of previous glacials rather than imposed patterns of its own. In the discussion which follows, a sequence of events described in terms of the last glacial may therefore be an over-simplification of the actual story. There will probably have been repeated separating, mixing, re-separating and re-mixing of stocks in the past, whereas it is only possible to attempt an explanation of the last, but much the most important, steps in the creating of the present picture.

Pleistocene Distributions

The walrus, *Odobenus rosmarus* (Fig 3)

The walrus exists in two easily recognisable subspecies, which were described as separate species by Allen (1880) and are more clearly differentiated than any other geographical races named as subspecies in the present review. The *divergens* race is extremely restricted in range and in numbers and is separated from the *rosmarus* group by a wide gap in North America between Point Barrow and Baffin Land and a smaller gap in Siberia between Chaun Bay and the Novosibirskie Islands. The continuity in distribution of the *rosmarus* group is interrupted because of the shore-dwelling nature of the species as a whole, and this group has suffered a marked recession of range in eastern North America in the last three centuries as a result of human interference.

Fig. 3. Distribution of the walrus, *Odobenus rosmarus*. The *divergens* race occupies the Bering Strait area and the *rosmarus* race occurs elsewhere. Districts where the species has been recently exterminated by man shown hatched.

The *divergens* and *rosmarus* races clearly originated as a result of glaciation and the consequent splitting of the species group, the former being pushed out into the North Pacific and the latter into the North Atlantic. Throughout historic times, *divergens* appears to have been consistently more numerous in the Asiatic part of its range than in the American part, and this, combined with the greater southward extension of ice on the Asiatic side, leads one to suppose that the southward movement during glacials was predominantly on the Asiatic side. A Pleistocene record exists for the Okhotsk Sea (Borissiak 1930). In the North Atlantic, however, not only is it likely from the disposition of ice that the population was split into eastern and western groups, but fossil

records exist for the Pleistocene of both North America and Europe. Most such records are listed in Kellogg (1922) under the name *Odobenotherium virginianum*. The animal's feeding habits, which limit it to relatively shallow water, mean that the North Atlantic population must have been concentrated along the coast of N. America in the general vicinity of Long Island, and on the European coast in the vicinity of S. W. Britain and this conclusion is supported by the fossil evidence. The fact that the American population has not subsequently proved distinguishable taxonomically from the Eurasiatic population implies that the Pacific and Atlantic stocks have been separated for a much longer period than were the east Atlantic and west Atlantic stocks. Although separation in any one glacial would always be longer between Pacific and Atlantic than between east and west Atlantic or east and west Pacific, it seems more likely on the morphological evidence that the separation between *divergens* and *rosmarus* dates from an earlier glacial and for some reason effective mingling of the stocks has not taken place since. In view of the apparent imminence of contact in the Arctic today, especially in Siberia, this conclusion may not appear a very likely one, but the answer may lie in the shore-frequenting nature of the species. Continued recession of sea ice and the dwindling of the permanent pack would not assist in the nucleation of the species as it would in the case of more pelagic species, and the two stocks might well have been left as remnant populations on interglacial shores. The last glacial would then have perpetuated and accentuated this differentiation.

The bearded seal, *Erignathus barbatus* (Fig. 4)

It is convenient to consider *Erignathus* next as, in some ways, it provides an interesting comparison with the last species. Two subspecies are generally recognised, *nauticus* from the Okhotsk and Bering Seas and *barbatus* which ranges in Arctic waters from the Laptev Sea of Siberia to the Beaufort Sea of Canada. Although Bobrinskii (1944) clearly indicates a gap between the two races in north-eastern Siberia, there is considerable doubt as to the status of the animals frequenting Alaskan shores. Not only have I been unable to determine whether the species is truly established throughout the area, but recorded specimens are referred to *nauticus* by Miller and Kellogg (1955) and to *barbatus* by Anderson (1946). Even so, the general picture is clear enough. The two subspecies represent two groups separated by glaciation, one having been pushed along the Asiatic coast to Northern Japan and the other having been pushed southward into the Atlantic. As in the case of the walrus, it seems reasonably certain the Pacific group moved primarily along the western side of that ocean, but in the Atlantic the probabilities are more difficult to assess. *Erignathus* is, like *Odobenus,* an animal of shallow waters, but it is a more northern form and capable of living beneath sea ice. It should have been able to maintain itself along the glaciated coasts of the seasonal pack zone, especially as sea level would have been lower than at present. The Atlantic group would then have remained fairly unified and no significant differentiation would be expected. A Pleistocene record for south-eastern England is listed in Kellogg (1922) and the species has been found subfossil in Sweden (Modén 1935). Since the last glacial, the *barbatus* group has followed the pack ice northward and has spread along the Canadian and Siberian coasts. On the other hand, the *nauticus* group has spread but little, and has largely remained in its probable glacial refuge, the Okhotsk Sea. Why the *divergens* race of *Odobenus rosmarus* has reinvaded the Arctic more readily than the *nauticus* form of the normally more northern *Erignathus barbatus,* is a problem to which I can suggest no answer at the moment. The difference of opinion about the taxonomic status of Alaskan bearded seals may be an indication that the two groups are now in process of meeting up again in this region and that a certain amount of genetic interchange is taking place. Morphological differences between the *nauticus* and *barbatus* races are very much less than between the subspecies

FIG. 4. Distribution of the bearded seal, *Erignathus barbatus*. The *nauticus* race occupies the Okhotsk-Bering Sea region and the *barbatus* race occurs elsewhere. Subspecific status of specimens obtained in the hatched area is not clear.

of the walrus, and it is reasonably certain that they derive only from separation in the last glacial age, previous separations having been nullified by intermingling during the last interglacial.

The ringed seal, *Phoca hispida* (Fig. 5)

Phoca hispida is possibly the only species capable of remaining in the arctic during glacials and may differ in that at least one of its subspecific forms probably arose in isolation within the Arctic basin. This is suggested not only by the potentialities of present day ecology, but also by the number of named forms within the Arctic. It is especially probable in the case of the Siberian coast, where glaciation was not so severe in the fourth glacial, and, in any case, *hispida* may have survived in the ice dammed Ob and Yenesei, as did the ancestors of *P. sibirica* and *P. caspica* (see below).

FIG. 5. Distribution of the ringed seal, *Phoca hispida*. Racial distribution indicated as follows: *hispida* ; *pomororum* ; *birulai* ; *ochotensis* ; *krascheninikovi* ; *beaufortiana* Others shown in black and named.

The glacial history of *P. hispida* is therefore the most difficult to reconstruct, but the explanation which follows seems to fit the available facts better than any other and would need only partial modification if some of the named races of *hispida* should subsequently prove invalid.

In the third interglacial, one more or less uniform group would have existed in the Arctic basin, around the remnant of polar sea ice. If separate subspecies had previously arisen they would have been eliminated by interbreeding in such a constricted range. With increased glaciation, the species spread peripherally, so that, at the height of glaciation, it probably occupied Davis Strait and the Greenland and Norwegian Seas in the North Atlantic, and the Bering and Okhotsk Seas in the Pacific. That it commonly occurred south to Scotland is confirmed by several specimens from Pleistocene deposits there (Kellogg 1922). In addition, a small population remained in North Siberia, either in the Kara-Laptev Sea area or in small ice-dammed lakes along the Ob and Yenesei Rivers.

With deglaciation, some of the Okhotsk Sea animals remained behind, becoming *ochotensis* and split from the Bering Sea population which spread northward back into the Arctic. Continued spread eastward along the Canadian Arctic coast gave rise to the *beaufortiana* group, but westward, along the North Siberian coast, the possible range was already occupied by seals which had remained behind in the Siberian Arctic and had become differentiated as the *birulai* group. That section of the population remaining in the Bering Sea then became the *krascheninikovi* group.

In the Atlantic, ice retreat saw a splitting of the previously unified Atlantic population into western and eastern groups. The western group was ancestral to the present day *hispida* and *soperi*. It spread northward, recolonising the eastern Arctic of Canada and meeting *beaufortiana*. The *soperi* population became isolated in Lake Nettilling, Baffin Island by post glacial uplift of land in relation to the sea and is therefore generally contemporary with *P. vitulina mellonae* (Fig. 11). It seems that it has since partially returned to the sea through the outlet to Nettilling Lake, as Anderson (1946) gives the east side of Foxe Basin as an additional locality. The *hispida* population also spread along the east Greenland coast to Spitzbergen.

The population in the east Atlantic was ancestral to *pomorорum, botnica, saimensis* and *ladogensis*. The initial separation was between *pomororum*, which followed the ice north along the Norwegian and Murman coasts into the White Sea, and the remainder of the group, which spread into the Yoldia Sea of Scandinavia, at that time covering parts of the present Baltic, Lake Ladoga and Lake Saima (Fig. 6). With the formation of the Ancylus Lake, this population was effectively isolated and, shortly afterwards, *saimensis* became separated. Finally, about the end of the Ancylus Lake period and the beginning of the Littorina Sea, *ladogensis* became isolated. Meanwhile, the *pomorорum* group was prevented from spreading far along the Siberian coast by early contact with the already present *birulai* group. Indeed, the conspicuously small progress eastward made by *pomorорum* could be advanced as a reason for believing that *birulai* ancestors had in fact

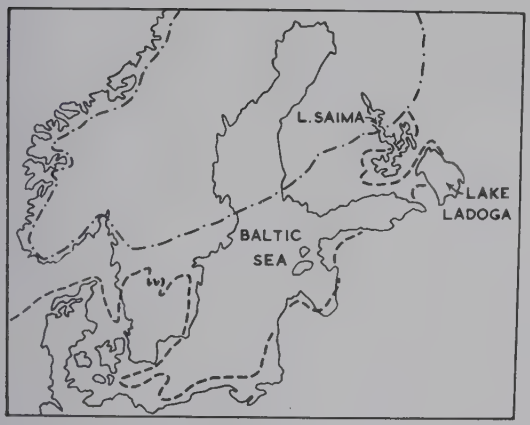
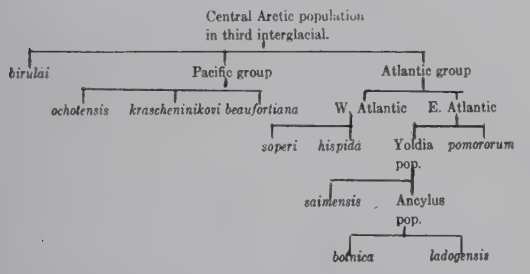


FIG. 6. The routes of entry of Baltic races of *P. hispida*. Approximate edge of contemporary Scandinavian ice sheet —•—• ; approximate Yoldia Sea shoreline – – – – (mainly after Sauramo).

remained in the Arctic during the fourth glacial. By analogy with other species, it is unlikely that *birulai* represents a reinvasion from the Pacific, since, in all other species, the Atlantic groups have made considerably more progress in reinvasion than have those from the Pacific.

The suggested relationship of *P. hispida* races is illustrated in Table II.

TABLE II. Suggested relationship of *Phoca hispida* races.



The Caspian seal, *Phoca caspica* and the Baikal seal, *Phoca sibirica*

It may not be an exaggeration to say that these two seals have attracted more zoogeographical attention than all other pinniped species put together. Obviously of Arctic origin and closely related to *P. hispida,* their isolation in two inland Asiatic seas has led to considerable speculation. The first undoubtedly correct explanation of their isolation appears to have been given by Piroznikov (1937) and the account which follows attempts to elaborate and to date the sequence of events.

The west Siberian ice sheet developed on the highlands of Nevaya Zemlya and the Taimir peninsula, between the Arctic Ocean and the great gulfs formed by the lower courses of the Ob and the Yenesei rivers. As the ice sheet grew, it dammed back these rivers forming large freshwater lakes. During the fourth glacial the water was probably dammed to form two small lakes in which the ancestors of *P. hispida birulai* may have survived, but the third glacial in Siberia was considerably more extensive and it is known that at this time one very large lake arose into which both the Ob and Yenesei flowed. As far as I am aware, the deposits formed by this lake have never been mapped and Figure 7 attempts to reconstruct it by using present topography and the edge of the ice sheet as given by Flint (1947, Fig. 64).

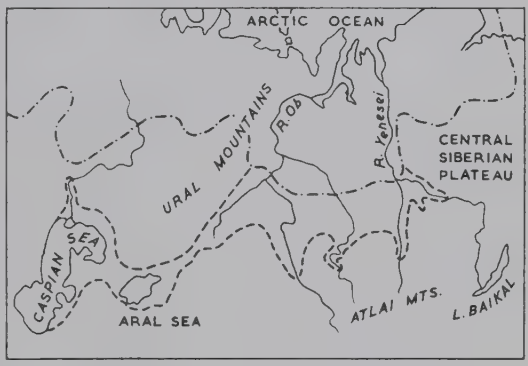


FIG. 7. The routes of entry of *P. caspica* and *P. sibirica*. Approximate edge of West Siberian ice sheet at climax of third glacial —·—·—·; attempted reconstruction of ice dammed lake – – – – – –.

The lake was connected through a strait at the head of the Tobol River with the Aral and Caspian Seas, which would then have been joined and it seems evident that this was the route by which *P. caspica* reached the Caspian. It is generally agreed that both *caspica* and *sibirica* are derived from *Phoca hispida,* although according to most authors they have now achieved specific rank. They must have originated from a *hispida* group which was present in the Ob and Yenesei gulfs and consequently became an inhabitant of the large ice-dammed lake. This population then split into three groups, one entering the Caspian to give rise to *caspica,* one entering Lake Baikal as the ancestor of *sibirica* and the third remaining in the lake and returning to the Arctic with the retreat of the ice, thus rejoining the main *hispida* population as a subspecies, which became eliminated by interbreeding during the last interglacial. There seems little doubt that this explanation, or some variation of it, is the correct one, but there is a possibility that a roughly similar sequence of events could also have taken place in one of the

first two glacials, since little is known of these in Siberia and the evidence for them may be concealed by that for the third. On present information, the third glacial looks to have been the most likely time except that it is still difficult to account for the entry of *sibirica* into Lake Baikal. Baikal is drained by the River Angara, which is a tributary of the Yenesei, but its present level is over 1,000 feet above the probable level of the ice-dammed lake and such a difference in level would have meant that the two water bodies must have been at least 600 miles apart. The Angara today contains numerous rapids.

The explanation lies in the upward movement of the central Asiatic highlands which was going on in the Pleistocene and which may have caused the surface of Baikal to rise about a thousand feet above sea level in the last 300,000 years. According to Gromov (1945), there was a significant orogenic phase in Siberia during the upper Pleistocene and, although no figures can be quoted, it appears likely that sufficient epeirogenic uplift occurred to bring this about. Bearing in mind the peculiar and restricted habitat, a date in the third glacial fits in well with the degree of differentiation which has taken place.

The harp seal, *Phoca groenlandica* and the ribbon seal, *Phoca fasciata* (Fig. 8)

Phoca groenlandica is the only species of *Phoca* which occurs in the Atlantic but not in the Pacific and *fasciata* is the only one which occurs in the Pacific but not in the Atlantic. I have long suspected that these two species are more closely related than is generally supposed and the considerations of the present study suggest that they may be the result of permanent separation of an ancestral group during the first or second glacial. The ribbon seal is little known and regarded as rare, but information recently given by Wilke (1954) suggests that it congregates for breeding on floating sea ice in the Okhotsk Sea, spreading out from here at other times of year, so that it occurs in very small numbers northward to the Bering and Chukchi Seas. In this it parallels *groenlandica,* which breeds on the edge of the North Atlantic pack and moves northward in summer. Both species are therefore generally pelagic in nature and inhabit the southern part of the zone of seasonal pack, replacing each other on either side of the Arctic. In size and external proportions, the species are very similar. They are the only two seals in which the pelage displays a banded pattern, although this pattern and the constituent colours are different in the two species. The coats of immature animals, however, are much more similar and may give a clue to the appearance of the ancestral type from which the males have diverged. Initial doubt as to whether *groenlandica* occurred in the Pacific resulted from confusion between the two species (Mohr 1952, p. 204).

FIG. 8. Distribution of the harp seal, *Phoca groenlandica* (Atlantic) and the ribbon seal, *Phoca fasciata* (Pacific). Known breeding areas ▬ ; out of breeding season distribution ////

Unfortunately, museum material referable to *fasciata* is extremely scarce and it is impossible to obtain any idea of the range of variation which exists. Doutt (1942), if I interpret him correctly, tends to group the two species together on cranial characters and certainly points to numerous similarities. The major dissimilarities are the broad and arched palate in *fasciata* and the more conical shape of the molar teeth. The external form of the teeth was primarily responsible for Gill's (1873) proposal of a separate genus, *Histriophoca,* for the ribbon seal, although this is now generally rejected by workers on the pinnipeds. Both the external form of the teeth and the form of the palate may be correlated with a divergence of diet between *fasciata* and *groenlandica.* The latter takes a considerable proportion of planktonic crustacea, while the very small amount of information available suggests that *fasciata* may be more of a specialised fish eater. Wilke (1954) records fish and squid from the stomachs of two specimens of this species.

Mohr (1951), after examining a skull of *fasciata* in Stockholm concludes that many details show a very close relationship between *fasciata* and *groenlandica* and that if it is necessary to place the latter in the genus or subgenus *Pagophilus* of Gray 1844, then *fasciata* must be placed with it, so that *Histriophoca* of Gill 1873 becomes a syno-

nym. Ecologic and zoogeographic considerations strongly support this view.

If *P. fasciata* and *P. groenlandica* originated by the separation of an ancestral group into Pacific and Atlantic stocks during the first or second glacials, it is necessary to explain their continued separation, since remixing in subsequent interglacials cannot have occurred. A possible explanation is that *fasciata* has remained a relic in the Okhotsk Sea. The role of the Okhotsk as a vast trap detaining northward gravitating species is closely similar to that of the Baltic on the Atlantic side of the Arctic. Both *Erignathus* and *Phoca hispada* have left behind what are essentially relic populations in the Okhotsk, as *Phoca hispida* and, for a short period, *P. groenlandica* did in the Baltic. The major difference has been that the Baltic is an ephemeral sea, covered by the Scandinavian ice sheet during glacials and changing its character rapidly in interglacial times. If the present rate of isostatic readjustment of land and sea levels continues, a few thousand years will see the further splitting up of the *Phoca hispida* and *Halichoerus* populations remaining there and their eventual extinction. The Okhotsk Sea has been much more static by comparison during the Pleistocene and it is not unlikely that relic populations dating from the first two glacials would survive to the present day, although probably in very reduced numbers as is the case with the ribbon seal. The *groenlandica* section of the original group must, during interglacials, have remained on the Atlantic side of the Arctic basin in the same way that *Cystophora* has done. These two species are found in close proximity today and are the most southerly of the regularly ice-frequenting forms.

During and since the last glacial age, *P. groenlandica* has become split into what appear to be three discrete breeding populations, which we may call the Newfoundland, Jan Mayen and White Sea groups. Not only do these groups breed in well defined areas, but they are also believed to summer in separate regions to the north. The White Sea group has been separated as subspecies *oceanica,* although it is doubtful whether it is more truly separable from the other two groups than they are from each other. At the height of the last glacial, the species would have been distributed along the edge of the seasonal pack and fairly well grouped together. As the ice retreated northward, isolation would become gradually more pronounced with the gaps in the seasonal pack at S.W. Greenland and Spitzbergen forming the operative barriers. The maximum degree of isolation would presumably have occurred at the postglacial thermal maximum, since when the ice has, on balance, spread slightly southward again. A fourth isolated group of *groenlandica* has ceased to exist. This entered the Baltic with the retreat of the ice sheets and the formation of the Yoldia Sea, became cut off in the Ancylus Lake and survived subsequently into the Littorina Sea. There it became extinct at about the time of the thermal maximum and with the assistance of Neolithic seal hunters (Clark 1946). In contrast, the more northern, but smaller, species, *hispida,* managed to persist.

The hooded seal, *Cystophora cristata* (Fig. 9)

This species differs from all the other members of the *Phocidae* mentioned in that it is a member of a separate subfamily, the Cystophorinae, which also includes the elephant seals of the Pacific and Southern Oceans. The subfamily is less clearly associated with the Arctic basin than are the Phocinae, although the extinct *Mesotaria* was European and lends weight to the probability of northern origin.

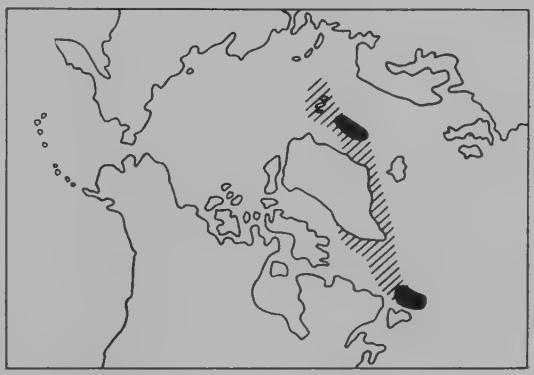


FIG. 9. Distribution of the hooded seal, *Cystophora cristata.* Known breeding areas ▬ ; out of breeding season distribution ////////.

Cystophora is a pelagic seal, frequenting the southern edge of the ice pack. As far as is known at present, it breeds in two well defined localities which are roughly the same as those occupied by *Phoca g. groenlandica,* although it does not move as far north as that species out of the breeding season. There is no evidence that it has ever become circumpolar and it is confined to the Atlantic today. The most noticeable characteristic of its present distribution is probably its western bias, since it has no eastern representative corresponding to *P. groenlandica oceanica.* This indicates a southwestward movement in glacial times.

The eastern limit of distribution of *Cystophora* is determined by an area immediately west of Spitzbergen where there is very little seasonal ex-

tension of pack ice. This is the gap between the "West Ice" and the "East Ice" of the sealers and it seems to have been important in the recent isolation of population groups. It divides *Phoca g. groenlandica* from *P. g. oceanica* and may also mark the division between *Phoca h. hispida* and *P. h. pomororum*.

The harbour seal, *Phoca vitulina* (Fig. 10)

Up to the present stage in this review, a reasonable degree of consistency has been obtained in the conclusions reached. The most northerly species, *Erignathus* and *P. hispida,* have clearly become circumpolar in each interglacial and their present differentiation is slight and dates from the last glacial. The next most northerly species, *Odobenus* has generally succeeded in becoming circumpolar, but probably not in the last interglacial, so that its differentiation seems to date from further back—probably the second or third glacial. Of the two most southerly ice-frequenting species, *P. groenlandica-fasciata* probably became circumpolar only in the first or second glacial and has not succeded since, so that differentiation is very advanced, while *Cystophora* has apparently not succeeded at all. To anticipate we may note that the boreal species, *Halichoerus, Eumetopias* and *Callorhinus* are also confined to one side of the Arctic and are unlikely to have existed elsewhere. There is thus a relationship between the degree of northerliness at present exhibited by each species, the extent to which it has become circumpolar and the age of its constituent differentiated forms. *Erignathus* and *P. hispida* subspecies are barely demonstrable, *Odobenus* subspecies are arguably worthy of specific rank and *P. groenlandica* and *P. fasciata* are clearly good species in the generally accepted sense, although it is to be doubted whether they would not interbreed and produce viable offspring. We must now turn to *Phoca vitulina,* which is a boreal species existing in the Pacific and Atlantic Oceans and thus proves the exception to the general rule.

Before discussing the geographical distribution and relationships of the *vitulina* forms, some of its ecological and taxonomic characteristics must be summarised. By almost all criteria, it is one of the most successful of pinniped species and certainly has the largest effective range. This extends from Japan, Baja California, Maine and France in the south to the Bering Sea, Hudson Bay and northern Norway in the north. In addition it makes seasonal journeys northward through Bering strait and to Ellesmere Island, Spitzbergen and Novaya Zemlya wherever ice-free waters can be found. It is to this readiness to move into the Arctic that we must probably look for an explanation of its presence in the two oceans. Although it is essentially a boreal species, it regularly invades the zone of seasonal pack to considerable distances and, in this way, contrasts with *Halichoerus,* especially in the west Atlantic region. Fortunately, the taxonomy of *Phoca vitulina* has been recently revised by Doutt (1942) and it is upon this work that the list of subspecies previously given is ultimately based. Pacific races can be separated from their Atlantic relatives by an almost constant cranial character—the projection of the premaxillaries backward along the nasals. The race *geronimensis* is separable by skin characters although no good distinguishing characters could be found in the skulls and the freshwater lake form *mellonae* is clearly distinguishable by both skin and skull characters. On the other hand, Doutt was unable to distinguish between *largha* and *richardii* of the west and east Pacific and between *concolor* and *vitulina* of the west and east Atlantic. He retained these races provisionally "until material sufficient to settle the matter can be obtained."

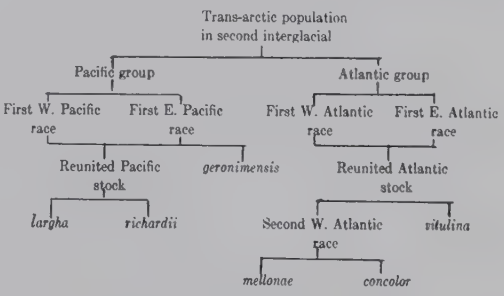
If we ignore, for the time being, *mellonae* which is rather a special case and better dealt with separately, the taxonomic conclusions of Doutt agree very well with what one would expect from zoogeographical considerations. If *vitulina* differentiation dates from the last glacial, then the sepa-

FIG. 10. Distribution of the harbour seal, *Phoca vitulina.* Racial distribution indicated as follows: *vitulina* ; *concolor* ; *richardii* ; *geronimensis* ; *largha* . Summer extension of range of *vitulina* and *concolor* races .

ration between Pacific and Atlantic groups would be slightly older than that between eastern and western groups in each ocean. The first advance of glacial and sea ice would separate Atlantic and Pacific stocks, while continued advance would push this boreal species down the east and west coasts of both oceans, thus forming four discrete groups. But there are three considerations which lead me to believe that this was accomplished in two glacial ages rather than one. First, a clear morphological difference has arisen as a result of the initial Pacific-Atlantic separation, whereas Doutt could find none resulting from east-west separation. This suggests that the first separation was significantly older than the second and that the Pacific and Atlantic stocks must have had a good length of time in which to acquire uniform characters before they were again split. Second, *vitulina* is a boreal form. Its trans-Arctic migration is exceptional when viewed in relation to other species and very favourable conditions would be necessary for it to achieve a circumpolar distribution. These could best occur in the second interglacial, which, although not shown to be significantly warmer than the others, is agreed to have been much the longest. Third, there is the necessity of accounting for *geronimensis* which seems to be more clearly differentiated from *richardii* than is *richardii* from *largha*. The presence of *geronimensis,* not separated by any well marked geographical barrier, can best be explained by two distinct southward movements of the species along the western coast of North America, *geronimensis* being the product of the first and *richardii* that of the second.

The explanation which best fits the facts of *vitulina* distribution and differentiation is therefore the following. Final separation of Pacific and Atlantic stocks occurred with the beginning of the third glacial, with the Pacific stock occupying the Bering Sea region and the Atlantic stock the region of Labrador-Greenland-Iceland-Norway. Further advance of the ice split both these stocks into two, so that in both oceans eastern and western stocks became isolated. In the third interglacial there was a species migration northward so that eastern and western stocks were reunited and were able to mix genetically over several thousand years, but somehow the *geronimensis* stock was left behind, or in some way became detached. Pacific and Atlantic stocks did not effectively meet during this interglacial. During the fourth glacial, eastern and western stocks were again created in each ocean and *largha* and *richardii* resulted in the Pacific, with *concolor* and *vitulina* in the Atlantic. Finally, in a late stage of glacial retreat, *mellonae* became separated from the main stock of *concolor*. The relationship between *vitulina* races would thus be as set out in Table III. With the retreat of the ice since the last glacial, *largha* and *richardii* are again in contact, since both are recorded from the Bering Sea. With further ice retreat, mixing will presumably take place once more.

TABLE III. Suggested relationship of *Phoca vitulina* races



No Baltic stock of *vitulina* has arisen. It has not penetrated further than the south-western corner of that sea and all evidence points to its relatively recent arrival, which has certainly been since the creation of the Littorina Sea.

The *mellonae* race remains to be discussed. This was described by Doutt (1942) from specimens obtained in Lower Seal Lake in Ungava, a freshwater lake about ninety miles from the coast of Hudson Bay. Although *mellonae* cannot possibly be other than postglacial in origin and was almost certainly trapped by successive partial submergence and emergence of the Ungava peninsula, it is clearly separable by both skin and skull characters from other *vitulina* races, presumably because the shortness of the period of isolation has been outweighed by the unusual and restricted nature of its environment. In *mellonae* skulls, the premaxillaries are not extended back along the nasals and on this score it is a member of the Atlantic rather than the Pacific stock, but Doutt noted slight resemblances to *richardii* which led him to investigate the possibility that *mellonae* came from the Pacific. He cites geological opinion that Hudson Bay may have been open to the north-west while still blocked from the Atlantic by glacial ice and also mentions the prevailing west-to-east set of marine currents. But geological opinion is very much divided on the first point and Flint (1947) says that entrance of the sea into the deglaciated Hudson Bay depression "must have been by way of Hudson Strait." The Geological Society of America's Glacial Map of North America (1945) shows very limited subsidence of Boothia and Melville peninsulas. The second

point is not a very strong one, as Doutt himself admits, since there is no evidence that seal distribution is in any way influenced by ocean currents, except in so far as they affect sea water temperatures.

On the other hand, there are two very good reasons for believing that *mellonae* is derived from the Atlantic. The first is that the Ungava peninsula is now within the range of *concolor,* whereas the nearest *richardii* seals are about three thousand miles away and, although there may have been some shrinkage of range since the postglacial thermal maximum, it is unlikely to have been of this order. In any case, the best evidence suggests that *mellonae* was isolated before the thermal maximum, when the climate would have been as cold if not colder than at present. The second reason is that there appear to me to be substantial grounds for believing that the seals are just as likely to have come from Ungava Bay as from Hudson Bay. The divide between streams flowing into these two bays is a very indeterminate one and this is especially true in the region of Lower Seal Lake. In fact it is so indeterminate here that Doutt's map appears to show Seal Lake as draining to both east and west, although the maps which I have been able to consult show a slight divide between the lake and the upper waters of the Stillwater River. Because of stream rejuvenation which must have taken place with the great recent rise of land relative to the sea, it is highly likely that there has been some drainage capture by streams flowing relatively steeply into Hudson Bay at the expense of streams flowing relatively gently into Ungava Bay. It is very possible therefore that the initial drainage of Lower Seal Lake was eastward into Ungava Bay as is still that of Lake Minto, immediately to the north, and which Doutt also shows as having a dual outlet. Fig. 11, based on the Glacial Map of North America, shows probable postglacial shorelines at the time of maximum submergence. The map is much generalised and not reliable in detail, but it shows that a long arm of the sea reached from Ungava Bay almost, if not quite to Seal Lake. The exact relationship between these water bodies is probably only determinable by expert geomorphological investigation on the spot, but is sufficiently doubtful to make it at least as possible that *mellonae* ancestors entered from Ungava Bay along the drowned Koksoak-Larch-Stillwater valley as by submergence of the Hudson Bay shorelands. Dunbar (1949) mentions that *P. vitulina* was once common in rivers flowing into the western side of Ungava Bay.

FIG. 11. Ungava peninsula and southern Baffin Land, showing the lakes occupied by *Phoca hispida soperi* (Nettiling) and *Phoca vitulina mellonae* (Lower Seal Lake). Postglacial emergence shown by diagonal lines.

The grey seal, *Halichoerus grypus* (Fig. 12)

I have reviewed the geography of the grey seal elsewhere (Davies 1957) and described its dif-

FIG. 12. Distribution of the grey seal, *Halichoerus grypus.*

ferentiation. It exists today in three well marked population groups which, although they have not been adequately examined morphologically, differ very much in breeding season and are obviously genetically isolated. *Halichoerus* is a boreal species, meeting ice only during late winter and early spring in the Baltic and Gulf of St. Lawrence. The split between west Atlantic and east Atlantic stocks would have occurred with southward movement of ice during the last glacial and the Baltic stock was separated by entering the Yoldia Sea and being trapped in the Ancylus Lake. There is no evidence that the species has ever occurred elsewhere than in the North Atlantic and its absence from the north Pacific is consistent with its boreal character.

The northern fur seal, *Callorhinus ursinus* (Fig. 13)

The Otariidae are apparently of Pacific origin and fossil forms have been found in the Miocene and Pliocene of Pacific North America. Although they may, during interglacials, have penetrated the Pacific side of the Arctic basin, there are no authentic records from the North Atlantic. The absence of trans-Arctic migration is what one would expect from the boreal and warm temperate character of the three species discussed here, none of which has any normal contact with ice. Their present distribution and differentiation reflects the effect of Pleistocene climatic changes within the North Pacific.

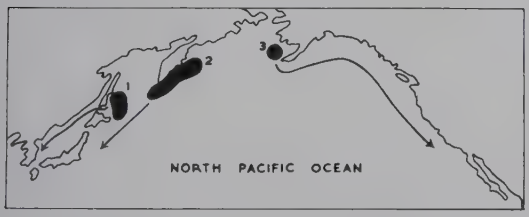


FIG. 13. Distribution of the northern fur seal, *Callorhinus ursinus*. Breeding distribution ▬ ; lines of migration ⟶ ; 1. *curilensis* race; 2. *ursinus* race; 3. *cynocephalus* race.

Callorhinus is primarily a boreal form, breeding in summer at the edge of the subarctic zone and making pronounced seasonal migrations southward to the edge of the warm temperate zone. It has been separated into three subspecies, the breeding grounds and main migration routes of which are shown by Fig. 13. It seems likely that the lines of migration of *cynocephalus* on the east and *ursinus* and *curilensis* on the west represent the lines along which population movements took place in response to the changing climates of the Pleistocene. Taking this view, it would appear that the fundamental division is between *cynocephalus* and *ursinus-curilensis* and that the two Asiatic races became isolated during a glacial period when separated by the Japanese islands as they are today in their winter quarters. In a species so intensely concentrated into a few very large colonies, it may well be that geographical differentiation reflects a barrier which operated at a time when species distribution was different from that at present. In the same way, the geographical barrier which gave rise to the *geronimensis* race of *Phoca vitulina* may have been one which operated at a time when species distribution was more southerly than at present and the peninsula of Baja California immediately suggests itself as such a barrier.

The breeding colonies of *Callorhinus* were almost certainly further north than at present during interglacials, but, because of the strong colonial attachments which appear to exist, this does not imply that mixing of eastern and western stocks readily took place. However, the results of tagging operations at the Pribilofs indicate that mixing is taking place today.

The northern sea lion, *Eumetopias jubata* (Fig. 14)

No subspecies of *Eumetopias* have been listed and colonies of this sea lion occur here and there from Vladivostok to southern California. It is a boreal species and its distribution coincides remarkably with the total range of *Callorhinus*. In spite of glacial separation, it is clear that eastern and western stocks have mixed freely during interglacials and have again resumed contact after the last glacial age.

FIG. 14. Distribution of the northern sea lion, *Eumetopias jubata*.

The California sea lion, *Zalophus californianus* (Fig. 15)

Zoogeographical consideration of this species is inevitably affected by the point of view taken as to the identity of the sea lion of Japan. By some authors this animal has been regarded as synonymous with *Z californianus* and by others with the Australian sea lion, referred to as *Neophoca cinerea* by Ellerman and Morrison-Scott (1951).

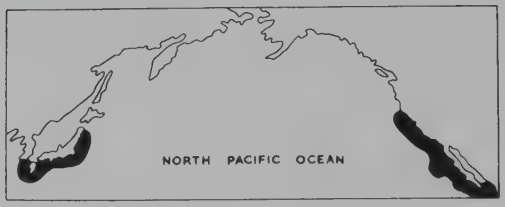


FIG. 15. Distribution of the California sea lion, *Zalophus californianus.*

The confusion which has arisen has, I believe, been satisfactorily cleared up by Sivertsen (1954), who shows that the Japanese and Californian sea lions belong to the same species. If Sivertsen's conclusion be accepted, as it is here, then the two population groups can be regarded as remnants of a former unified population separated by southward movement during glacial ages and not subsequently reunited. It need hardly be said that, from a zoogeographical point of view, the possibility of synonymy between Japanese and Australian sea lions represents a considerably greater problem and one to which it would be difficult to see an acceptable solution.

Zalophus is warm temperate in distribution and is not found where sea temperatures drop below 10°C at any time of year. It has been recorded from the Pleistocene of California (Kellogg 1927) and Japan (Matsumoto 1930 and 1939) and its amphi-Pacific distribution must date from a time when one united species group was spread across the North Pacific in the vicinity of the Aleutians. If present day temperature tolerances were then operative, this would necessitate an increase in winter sea temperatures of about 7° or 8° C near the Aleutians. It is extremely unlikely that changes in sea temperature of this magnitude took place during the Pleistocene and it is difficult to escape the conclusion that the species has gravitated towards a warm water environment since the time of separation of the two groups. The separation would then have been a comparatively early one, since when the two groups have remained separated if we may judge from their present distribution. A detailed morphological comparison between the Japanese and Californian groups would be of great interest in this regard.

SUMMARY

Present day distribution and differentiation of northern pinnipeds reflects the periodic expansions and contractions of sea and glacier ice which occurred during the Pleistocene. Considerable limitations were imposed upon seal distributions, from which it is possible to attempt a reconstruction of past ranges in spite of the general lack of fossil evidence. General relationship to sea temperatures and the presence of seasonal pack ice are considered the most important guides but were susceptible to variation. Feeding habits are of secondary importance as an indication of probable past distributions but were more stable.

Expansion of glacial and marine ice pushed seal populations southward, tending to split Atlantic from Pacific populations, to separate populations on either side of those two oceans and to isolate small population groups in lakes and partially land-locked seas. Contraction of the ice led to general northward movement, when previously isolated stocks would tend to regain contact and mix, although some were left behind as relic groups which sometimes survived and sometimes became extinct. These processes were probably repeated in each glacial age, but the last two, and especially the last, appear primarily responsible for the present pattern.

The most northerly species, *Phoca hispida* and *Erignathus,* have become circumpolar in each glacial and their Pacific and Atlantic representatives are little differentiated. The subarctic species have not always become circumpolar: *Odobenus* differentiation seems to date from the second or third glacial, *P. groenlandica* and *P. fasciata* appear to be the result of splitting in one of the first two glacials and *Cystophora* appears never to have become circumpolar at all. Boreal and warm temperate species are confined to either the Atlantic or the Pacific, with the exception of *P. vitulina,* which today makes summer excursions into the subarctic and probably became circumpolar in the long second interglacial.

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EFFECTS OF X-IRRADIATION ON A NATURAL POPULATION OF THE DEER-MOUSE (*PEROMYSCUS MANICULATUS*)[1]

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The work reported here was undertaken to learn the effects of irradiation on a natural population of a vertebrate. It consists of a simple experiment in which the mutation rate in a natural population was increased through irradiation with the intention of upsetting the equilibrium between mutation rate and selective elimination of deleterious mutants. The animal studied was the deer-mouse (*Peromyscus maniculatus*). A population was located about two miles south of Taylor, Williamson County, Texas, and was brought under observation by the use of nest boxes. Males from the population were brought into the laboratory, given gonadal dosages of x-ray, and then were returned to the population. The work was begun in the fall of 1951, and was continued until the spring of 1956. A control plot was also kept under observation beginning with the fall of 1954.

Field assistants on the project included: Jack A. Herrmann, Homer W. Phillips, Wilmot A. Thornton, William F. Pyburn and W. Newman Bradshaw. I am tremendously indebted to Mr. Louis Lannen for permission to do the field work on his property. Some of the irradiation was done at the Radiobiological Laboratory of the University of Texas, and for this courtesy I am indebted to George M. Krise, John A. Auxier and Loren C. Logie. I am indebted to Wilson S. Stone for reading the manuscript.

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Methods

The field work was done on an intensively cultivated, blackland prairie farm. The area on which the nest boxes were placed measured nearly one mile (5175 feet) in length and about 3675 feet in width. The boxes were placed along fences around most of the periphery of the area and along the few cross fences and uncultivated areas within the farm. Sale of two segments of land by the owner resulted in the loss of these areas from the study. One of these was lost in the southwestern corner before the 1954-55 season, and the other was lost on the eastern side before the 1955-56 season.

Nest boxes of the type described by Howard (1949) were used. The mice would use the boxes only during the colder six months of the year (November-April). Local farmers reported that the mice live in deep drought cracks in the black calcareous soil in the summer. Scorpions and ants occurred commonly in the boxes, and in a few instances deer-mice were stung by scorpions, without permanent harm to the mice. The most common mammals other than deer-mice in the boxes were wood-mice (*Peromyscus leucopus*) and house mice (*Mus musculus*). One harvest mouse

(*Reithrodontomys montanus*) and one shrew (*Cryptotis parva*) were found there. Other vertebrates found occasionally in the boxes included: fence lizards (*Sceloporus undulatus*), blue racers (*Coluber constrictor*), coachwhips (*Masticophis flagellum*), king snakes (*Lampropeltis calligaster*), Mexican toads (*Bufo valliceps*), spotted chorus frogs (*Pseudacris clarki*), and tiger salamanders (*Ambystoma tigrinum*).

The nest boxes were checked routinely by a field assistant, usually once or twice a week. The mice were marked by a toe-clipping and ear-punch system, and on each visit to a box the mice present and the number and estimated age of any litters of young were recorded. In all except the 1951-52 season sexually mature males were brought once to Austin for x-ray dosage. The mice were held in a wire cone and the body was shielded by a lead plate during dosage of the gonads with a total of 500r at rates of 90 to 100r per minute. Each mouse was then returned to the nest box from which it had been taken. The percentages of the males of marking age which were irradiated in each of the four years of dosage were as follows: 1952-53, 49.4%; 1953-54, 52.9%; 1954-55, 95.0%; 1955-56, 77.6%. The mice were not irradiated until they had reached sexual maturity (two weeks or more after marking), and this accounts in part for the year to year variation in percentage dosed. Some mice, of course, disappeared in the interval between marking and the time they would have become sexually mature.

The control plot which was followed through the last two years of the study was of little value, because the population density was very low in comparison with the study area. Ten mature mice were recorded on the control plot in 1954-55, and nine were recorded there in 1955-56.

Biology of the Deer-Mouse in Central Texas

Certain features of the ecological life history of the deer-mouse, as revealed by the field work, are pertinent to the present discussion. These include breeding season and the related population densities, localization of individuals in a home range, and dispersal distances of young mice.

Breeding Season

The deer-mouse is a winter breeder in central Texas. There is little or no reproductive activity in the hot months, and the population drops to a very low level at that season. Trapping in the summer, when the mice would not use the nest boxes, was attempted but discontinued because of the very small numbers of mice caught and because of the deleterious effects of trapping the mice in hot weather. Tabulation of the number of litters recorded in the nest boxes shows that reproductive activity begins in November, usually reaches a peak in February, and generally ceases by or before mid-April (Table I). The records for 1954-55 and 1955-56 need explanation. The absence of litters in the early months of winter indicates an absence of mice from the boxes rather than a lack of reproductive activity. The mice were slow to move into the boxes in those years, possibly because of climatic conditions, and when they did start to occupy the boxes young of the year were present in the population.

Table I. Litters of deer-mice recorded in nest boxes by two-week periods

Period	Seasons					Totals	
	1951–52	1952–53	1953–54	1954–55	1955–56	Total	% of all
Nov. 24-Dec. 6	..	5	4	..	..	9	8.2
Dec. 7-20	..	5	5	..	..	10	9.1
Dec. 21-Jan. 3	..	5	4	..	..	9	8.2
Jan. 4-17	3	2	3	..	..	8	7.3
Jan. 18-31	1	..	5	..	2	8	7.3
Feb. 1-14	..	2	7	..	4	13	11.8
Feb. 15-28	10	3	7	2	3	25	22.7
Mar. 1-14	..	..	4	2	4	10	9.1
Mar. 15-28	3	..	2	1	2	8	7.3
Mar. 29-Apr. 11	..	..	..	..	2	2	1.8
Apr. 12-25	..	..	..	5	3	8	7.3
Totals	17	22	41	10	20	110	100.1

A female which lives through the breeding season may have at least four litters. In fact, in some instances females born in early fall which survived to March produced four litters. The Texas mice, therefore, produce at least two generations per breeding season by comparison with the four generations per season reported by Howard (1949) in Michigan.

The numbers of mice recorded in the boxes give an indication of the build up in numbers in the winter months (Fig. 1). The irregularities in the curves apparently result from the effects of climatic conditions on occurrence of the mice in the nest boxes. For this reason, only the general trend of the curves is significant. The peak of the population curve, as reflected in the number of mice in the boxes, was usually reached in January or February. The specific dates are: February 26, 1952, January 3, 1953, February 3, 1954, February 15 and 24, 1955, and March 24, 1956. With the end of the winter breeding season, the population evidently declined sharply and remained at a low level through the summer.

The carryover of marked mice from one season to the next was very low, and the population at the start of the breeding season in the fall evidently consisted mostly of mice born too late in the spring to have been marked in the boxes. Four marked males survived from the 1951-52 to

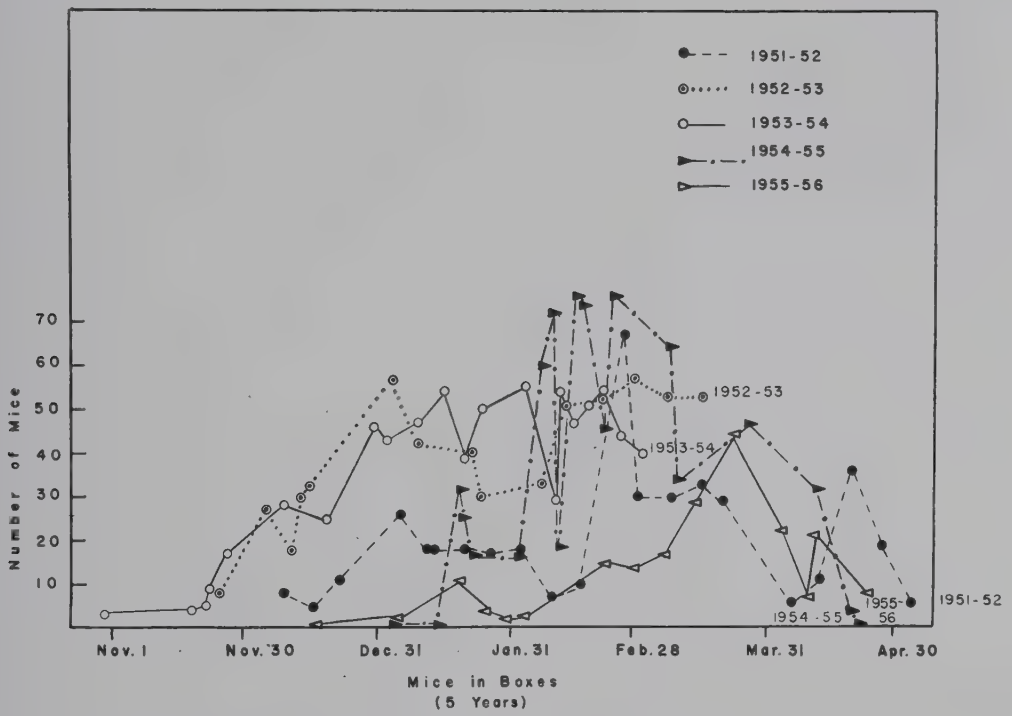

FIG. 1. Numbers of deer-mice found in nest boxes over five seasons of study. A smaller number of boxes on a smaller area was involved in 1955-56 than in the other seasons.

the 1952-53 season. None survived from the latter season to 1953-54. Three males marked in 1953-54 were recorded in the 1954-55, and none marked in 1954-55 was recorded in 1955-56.

Dispersal

The distance which young mice disperse before becoming sexually mature should have an important bearing on the outcome of the present experiment. A high rate of dispersal might result in the population on the study area being maintained through immigration in the face of deleterious effects of the irradiation. Extensive dispersal would also result in the spreading of radiation-induced genetic changes widely in the population, and extensive immigration would retard fixation of radiation-induced mutations.

Examination of the available dispersal records of mice which were marked in the box with the female parent shows that most of them disperse short distance or not at all (Fig. 2). The pattern of dispersal compares rather closely with what Howard (1949) found in this same species in Michigan. The somewhat higher percentage of both males and females which showed essentially no dispersal in my results than in Howard's may result from different mechanics of handling the data than from any real difference in the behavior of the mice. My data include all mice which were still present two weeks after marking (age of five to six weeks), by which time sexual maturity is reached in these mice. Thirty-eight males and an equal number of females were never recovered, and they presumably were taken by predators or possibly dispersed beyond the limits of the area.

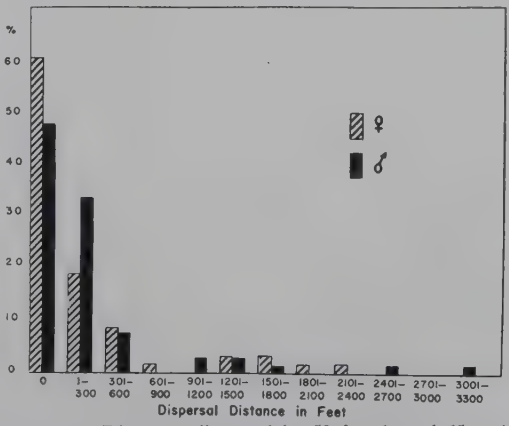

FIG. 2. Distances dispersed by 58 female and 65 male deer-mice which were found with the mother and later recovered at an age of five or more weeks.

The longest dispersal of a female recorded was 2240 feet, and the longest for a male was 3200 feet.

Social Behavior

The social behavior of the mice is very similar to that reported by Howard (1949) for the same species in Michigan. A male and female usually form a relatively permanent pair, which persists until one individual disappears from the area. The paired mice may remain in a single nest box, or they may move about together among two or three adjacent boxes. A social aggregation in a box may include a male and female and a suckling litter, or even all or part of a previous litter along with suckling young. The male may be absent from the box on a particular date but be back there at a later one. Some aggregations are more complex, involving more than one breeding animal of each sex. One detailed example will illustrate these complex aggregations. Nest box number 84 was checked nine times between February 22 and April 24, 1956. On February 22, pregnant ♀ 222 and recently suckling ♀ 223 were present with adult ♂ 197. On February 29, the same three were present, and ♀ 222 had a new litter of two young. On March 2, the same three were present; ♀ 223 had a new litter and was nursing one of the two young of ♀ 222 along with her own. On March 14, ♀ 222 was present with one of her two young, and ♀ 223 was there with her litter. On March 24, ♀ 223 was there with her three young, and ♂ 197 and adult ♂ 230 were also present. On April 4, ♂ 197 and juvenile ♂ 291, of unknown origin, were in the box. On April 12, ♀ 222 with two young (not newborn) and ♂ 197 were there. On April 24, only ♀ 222 and her three young were present.

Sexually mature mice remain in the same limited area through the remainder of their lives. The present method does not permit estimation of the size of the home range, but indications are that it is small and comparable to the home range sizes reported for the species in Michigan by Blair (1940) and Howard (1949). The home range habit and the habit of forming relatively permanent pairs permit one to obtain at least circumstantial evidence as to the male parent of a litter born to a female living in a nest box.

Results

With at least two generations produced per year and under the practice of dosing the males as they reached sexual maturity, a mouse born in the spring of 1956 could theoretically have five male ancestors which had each received 500r of x-ray dosage. The number of treated ancestors would be seven instead of five except for the fact that the mice did not move into the boxes early enough in the fall of 1954 and 1955 for the first generation of those years to be treated. In addition, the high degree of inbreeding indicated under the social system which prevails in these mice would be favorable to fixation of radiation-induced mutations in the population.

No visible mutations affecting pelage color or other morphological characters were detected. Three females in 1953-54 which associated with irradiated males each produced a litter of young in which the skin was dry and covered with dandruff-like scales, and one of seven young born to another female associated with an irradiated male was of this same type. A similarly affected litter was born in the 1954-55 season to a female associated with a treated male. This skin condition was possibly the result of radiation-induced genetic change affecting the physiology of the animals. All members of one litter survived at least to marking age, and the others were born too late in the season for any follow up on their fate.

One possible effect on the population would be the reduction in litter size as the result of radiation-induced lethal mutations. Dominant lethals would be expressed in the first generation following irradiation, of course, and recessives could be expected to be expressed in subsequent generations in an inbred population such as this.

The number of young in 31 litters produced in 1952-53 and 1953-54 by females associated with non-irradiated males averaged $5.03 \pm .18$ individuals. In the same period, 20 litters born to females associated with irradiated males averaged $3.86 \pm .41$ young. This latter calculation excludes two litters of three and five young, respectively, in which the young were born dead or died soon after birth. The difference between the two means is $1.17 \pm .40$, which is significant beyond the one per cent level. In the two following years no attempt was made to discriminate between litters born to irradiated and non-irradiated fathers, as all mice in the population possibly had four to five irradiated male ancestors in their family history. Eight litters recorded in 1954-55 averaged 3.87 young per litter, and eight recorded in 1955-56 averaged 3.62 mice per litter. The latter calculation excludes one litter of two which was born dead or died soon after birth. The reduction in litter size is comparable to what has been found in house mice and other laboratory rodents (see Russell 1954).

One of the chief effects on the population might be expected to be a change in population numbers if radiation-induced genetic changes were sufficiently great to impair the equilibrium between mutation pressure and selection pressure. Population numbers can be expressed most precisely in

a nest-box study such as this in terms of the number of mice which reached the age of approximately three weeks. This is roughly the age of weaning, and mice in the boxes were marked by toe-clipping at approximately this age. The number of mice known to have reached three weeks or more of age on the plot in four years and on a segment of it in five years is shown in Table II. The dual presentation is necessary because a major segment of the area was sold by the owner and became unavailable for study after the summer of 1955. A small corner was similarly disposed of in the summer of 1954, but the area was so small that realignment of the boxes bordering the area probably compensated for its loss.

TABLE II. Total number of deer-mice known to have reached three weeks or more of age on experimental area in five seasons

Period	On whole plot(4 years)	On smaller area followed 5 years	Remarks
1951-52.....	180	43	No irradiation
1952-53.....	153	57	49.4% ♂/500r gonadal
1953-54.....	173	59	52.9% ♂/500r gonadal
1954-55.....	171	103	95.0% ♂/500r gonadal
1955-56.....	...	86	77.6% ♂/500r gonadal

The population on the experimental plot, as judged by the number reaching weaning age, showed no changes other than those which might be attributed to random fluctuations (Table II). The variation from year to year was greatest on the small area that could be sampled throughout the five years, which is what would be expected as the result of random variation. There was remarkably little variation on the whole plot over the four years for which records could be made. There were only nine fewer mice recorded in the third year of irradiation (1954-55) than were recorded in the year in which there was no dosage (1951-52). The sex ratio remained even within the limits of chance variation throughout the period of study.

DISCUSSION

The details of the genetic effects of irradiation on the population can only be assumed in the present study. As pointed out by Muller (1954) mutations, either spontaneous or induced, occur in a kind of spectrum, with a narrow band of mutations with visible effects, a broad band of lethals to one side, and a broad band of mutations with invisible effects to the other. The reduction in litter size in the first generation following irradiation is attributed to the action of dominant lethal mutations, and it may be reasonably assumed that there was concomitant induction of mutations in the invisible band of the spectrum.

The untreated deer-mouse population was undoubtedly existing in equilibrium between its (unknown) spontaneous mutation rate and selective elimination of deleterious combinations. The effects of irradiation on the population, then, have been to increase the mutation rate. As Muller (1954) has pointed out, "It is not known how much permanent increase in mutation rate any given species is capable of enduring without decreasing in numbers and finally dying out, but each species has its own limit, determined by the magnitude of its original mutation rate and the rapidity with which it can replace lost numbers by selective multiplication." Muller (*op. cit.*) has called the level at which the mutation rate exceeds the ability of the species to tolerate it the "critical mutation rate." The maintenance of its population numbers by the deer-mouse through four years of irradiation and through at least eight generations suggests that its critical mutation rate must indeed be high.

The high critical mutation rate indicated for the deer-mouse is probably related in large part to the ecologic position of the species. Deer-mouse populations, like populations of other small mammals, exist under tremendous selection pressure, particularly from predators (Blair 1953). The life span in nature is only a fraction of the potential life span, and only a small fraction of the young mice produced ever reach sexual maturity. Howard (1949) found in Michigan that only one-fifth of the deer-mice born lived to sexual maturity. Blair (1948) found in Michigan that the life span of deer-mice which lived to leave the nest averaged less than five months, although the potential life span as indicated by caged individuals is several years. Selective elimination of deleterious genetic combinations should be highly effective under such conditions of predator pressure on the population, and it is believed to be largely responsible for the ability of the species to maintain itself under the conditions of the experiment.

Replenishment of the population through immigration from outside the experimental area must be considered as a possible factor in maintenance of population numbers. Inability to follow the mice through late spring and summer makes it impossible to determine genealogies, so evidence must be sought from other sources. The limited distance that young mice disperse (Fig. 2) provides the strongest argument against immigration having more than minor influence on maintenance

of the population. Also, the deer-mouse is relatively spotty, or at least uneven in population density, in the area of the study, and attempts to find a suitable control population resulted in the finding of no area with a density comparable to the one studied. The apparent reduction in litter size in the whole population in the last two years of the study would also argue against immigration playing a significant role in maintaining the population, as this reduction must be attributed in part at least to inbreeding of mice belonging to irradiated lineages. Study of a completely insular population would be required, of course, to rule out all possibility of immigration playing a role in maintenance of the population. In the present instance, we do not mean to imply that there was no immigration into the area, but we do believe that it played a relatively insignificant role in the maintenance of population numbers.

The exact mechanics of population maintenance in spite of reduced litter size cannot be proved by the evidence at hand. Slightly greater survival of the fewer offspring produced could account for it. A slight increase in the number of litters could also produce the same result. Direct comparison of number of litters between years is difficult because of differences in occupancy of the boxes in different years and because of the necessary reduction of the plot in the last year. The litters produced in January and February can be compared among the first four years, and were: 1951-52, 12; 1952-53, 12; 1953-54, 23; 1954-55, 2. These variations, however, probably indicate only differences in peaks of reproduction. In 1954-55, when only two litters were recorded in the two-month period, the mice did not move into the boxes until the first of January. Many of the mice which moved into the boxes then were juveniles, which indicated an earlier peak of activity.

Summary

An attempt was made to upset the equilibrium between mutation pressure and selection pressure in a natural population of deer-mice (*Peromyscus maniculatus*) through irradiation of sexually mature males. The work was done in central Texas, where a population was kept under observation by use of nest boxes. After one year of observation in 1951-52, exposure of males to a 500r gonadal dose of x-ray was begun and continued through 1955-56.

Certain aspects of population dynamics were highly pertinent to the conduct of the experiment and to the results obtained. Deer-mice are primarily winter breeders in central Texas. Relatively permanent mating pairs are formed. The average dispersal distance of the young is short. The life span is short and population turnover high, indicating high environmental pressure on the population.

Reduction in litter size is attributed to radiation-induced lethal mutations. Maintenance of population numbers through four years of irradiation is attributed to high selection pressure, and a consequently high "critical mutation rate" in a species such as this.

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THE EFECTS OF LARVAL CROWDING AND BODY SIZE ON THE LONGEVITY OF ADULT *DROSOPHILA MELANOGASTER*

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A series of experiments on the factors affecting duration of life in adult *Drosophila melanogaster* led Pearl (1922) to conclude that organisms have an "inherent vitality" which is their potential capacity to survive in the absence of external sources of matter or energy, that duration of life varies inversely with energy expenditure, and that inherent vitality may be expressed as rate of growth or duration of life. These conclusions are consistent with Rubner's hypothesis that the total

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energy transformed per unit of body weight is approximately constant and that duration of life is a function of the rate at which this total amount of energy is used.

By measuring the longevity of starved flies under different conditions of crowding, Pearl and his associates obtained the fellowing experimental evidence for the conclusions enumerated above: (1) females lived longer than males, (2) large flies lived longer than small flies of the same sex, (3) duration of life varied inversely with temperature, and (4) duration of life varied inversely with adult population density, although there was an optimum density of 35 to 55 flies per bottle above and below which longevity decreased. This evidence and Pearl's subsequent conclusions are the essential elements of his "physiological longevity" concept, in which he postulated that the lengevity characteristics of starved flies are an index of "ecological longevity." In other words, Pearl assumed that the lengevity relationships established with starved flies apply also to normal conditions, except that the negatively skew rectangular survivorship curve he obtained with starved flies would be depressed toward a diagonal type as a function of various ecological forces of mortality (Pearl 1922).

Since Pearl's conclusions rest partly on certain untested physiological and ecological assumptions, it would seem appropriate to establish (1) whether the rate of energy transformation during life is constant, (2) whether increased metabolic activity has an adverse effect on lengevity, and (3) whether the longevity performance of starved animals is in fact indicative of longevity under normal conditions. Furthermore, it has been widely assumed from Pearl's results that crowding has an adverse effect on lengevity, even though his experiments did not account for the larval history of the flies (Wright 1928). While adult *Drosophila* may compete to some extent for food and breeding sites, it is unrealistic to believe that competition for space, as represented in Pearl's experiments, is a serious factor in their ecology. If significant competition were to occur in nature, it would more probably be during the larval stages.

There is ample evidence that the rate of energy expenditure varies as a function of body size and temperature (Roder 1953), but there is no support for the assumption that the total energy transformed per unit of body weight is constant and, indeed, Northrop (1926) has shown that populations of *D. melanogaster* kept at different temperatures during adult life produce different total amounts of carbon dioxide. Secondly, even though crowding presumably causes an increase in activity and therefore metabolic rate, adult crowding does not have a consistent effect on lengevity (Pearl, Parker & Miner 1927). We must therefore regard the first of these assumptions as disproven and the second as doubtful.

The purpose of the present study was to test the ecological assumptions of the physiological longevity concept by measuring the effects of larval crowding and corresponding decreases in adult body size on the longevity of uncrowded, fully-fed adult *Drosophila melanogaster,* comparing the longevity relationships of normal flies with those established by Pearl for starved flies. It should be emphasized that this study makes no assumptions and comes to no conclusions regarding causes of mortality or the possibility of selection for resistance to crowding. For the purpose of these experiments, larval crowding may be regarded as a method for producing adult flies of different size or, conversely, we may state that the adults were products of different degrees of intraspecific larval competition and therefore differed in their nutritional histories (Chiang & Hodson 1950), but the relationship between body size and longevity was the only relationship tested.

We would like to acknowledge the statistical advice of Dr. C. L. Chiang and to also extend our appreciation to Mr. Charles Elton and Mr. P. H. Leslie who read the manuscript. This research was made possible by a grant from the American Academy of Arts and Sciences.

Methods and Materials

Inbred stocks of a Florida strain of *D. melanogaster* were obtained from Dr. J. A. Moore at Columbia University and further inbred for four generations at the Biological Laboratories, Harvard University. Parental stocks were selected for maximum size and fecundity (Chiang & Hodson 1950) and kept in population bottles where the females were allowed to oviposit on a clear medium of agar, sugar, and water. Early-first-instar larvae were collected from the surface of the egg-laying medium within four to six hours after hatching and were then transferred at appropriate experimental densities to eight-dram vials containing 5 cc of a standard medium (Kalnus 1943) and 1/20 cc of a 15% suspension of yeast and distilled water. The cultures developed at 25°C and 75-80% R.H. and adult flies were collected at 12-hour intervals during the period of emergence. The experimental densities for the larval cultures were 5, 10, 20, 40, 60, 80 and 100 larvae per vial, or 5 cc of medium. Previous experience with this culture method showed that these densities would produce significant size dif-

ferences in the adults without seriously altering the mortality rates of the larval populations.

The responses of *Drosophila* cultures to the forces of larval competition may be outlined very briefly as follows (Chiang & Hodson 1950; Sokoloff 1955): (1) an increase in the time required for larval development, (2) a decrease in larval, pupal, and adult body size, and (3) a decrease in the number of individuals that pupate and emerge as adults. Females tend to complete their development and emerge slightly sooner than males, but the majority of the population will emerge within a period of two days unless crowding has been extreme. Flies that emerge during the first two days are usually quite uniform in size, whereas those that emerge on the third and subsequent days in severely crowded populations often vary considerably in size (Chiang & Hodson 1950). Since one purpose of this culture method was to obtain flies of uniform size, only those flies that emerged on the first or second day were used in these experiments.

The longevity of seven populations of adult *D. melanogaster* reared from larval cultures with initial densities of 5, 10, 20, 40, 60, 80 and 100 per vial was tested at 25°C and 75-80% R.H. At each collection the newly emerged flies were lightly etherized, sexed, and transferred to eight-dram vials containing the same amount of food and medium as that used for the larval cultures. The initial adult density in each vial was five and the sexes were kept separate. The adults collected during a two-day period from a single larval culture were grouped as a population of "uniform age," even though their times of emergence might differ by as much as 48 hours. Samples of 10 to 20 flies from each population were weighed to the nearest 0.01 mg and their mean weights regarded as representative of the population.

Every five days the flies were shaken into vials of fresh food and medium, the dead flies discarded, and the number alive in each vial recorded. No attempt was made to keep the density in each vial constant once flies had died and the number in a particular vial had fallen below the initial density of five. Although this procedure may have been a factor in the results, its effect was minimized by selecting an initially low adult density.

Results

The relationship between larval density and adult body size is shown in Table I and Figure 1. Increased larval crowding produced non-linear reductions in body size, with maximum total reductions of 36.4 percent for males and 48.6 percent for females.

Mortality data for each of the adult populations

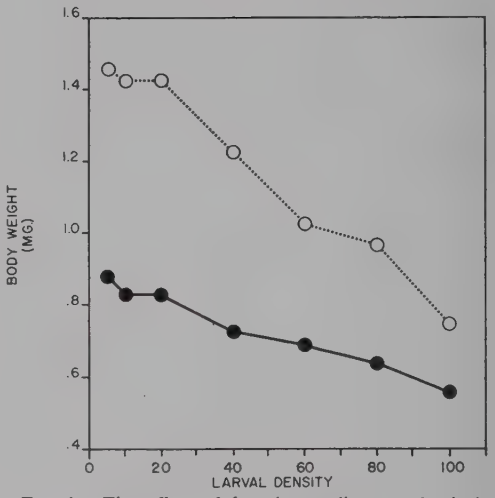

Fig. 1. The effect of larval crowding on the body weights of adult *Drosophila melanogaster*. Males, dots; females, circles.

Table I. The effect of larval crowding on the body weights of adult *Drosophila melanogaster*

Larval density	Males	Females
5	0.88 mg	1.46 mg
10	0.83	1.43
20	0.83	1.43
40	0.73	1.23
60	0.69	1.03
80	0.64	0.97
100	0.56	0.75

are shown in separate life tables (Table II a-g) which include the number alive at the beginning of each interval (l_x), the number of deaths during each interval (d_x), the mortality rate for each interval ($1000q_x$), and expectation of life at the beginning of each interval (e_x). Survivorship curves (l_x) are illustrated for each of the populations in Figure 2 a-g. The reader may refer to Deevey (1947) or Allee *et al.* (1949) for information about the construction and interpretation of ecological life tables and curves. The life expectancy at the beginning of the experiment is a particularly useful function and is defined as the total number of days lived by all flies, divided by the initial number of flies. Life expectancy at the beginning of the experiment, denoted as $\overset{\circ}{e}_o$, may be computed from the following formula:

$$\overset{\circ}{e}_o = \times \frac{1}{2} + \frac{l_1 + l_2 + \ldots . l_n}{l_0}$$

$$l_o = 5 \frac{1}{2} + \frac{l_1 + l_2 + \ldots . l_n}{1000}$$

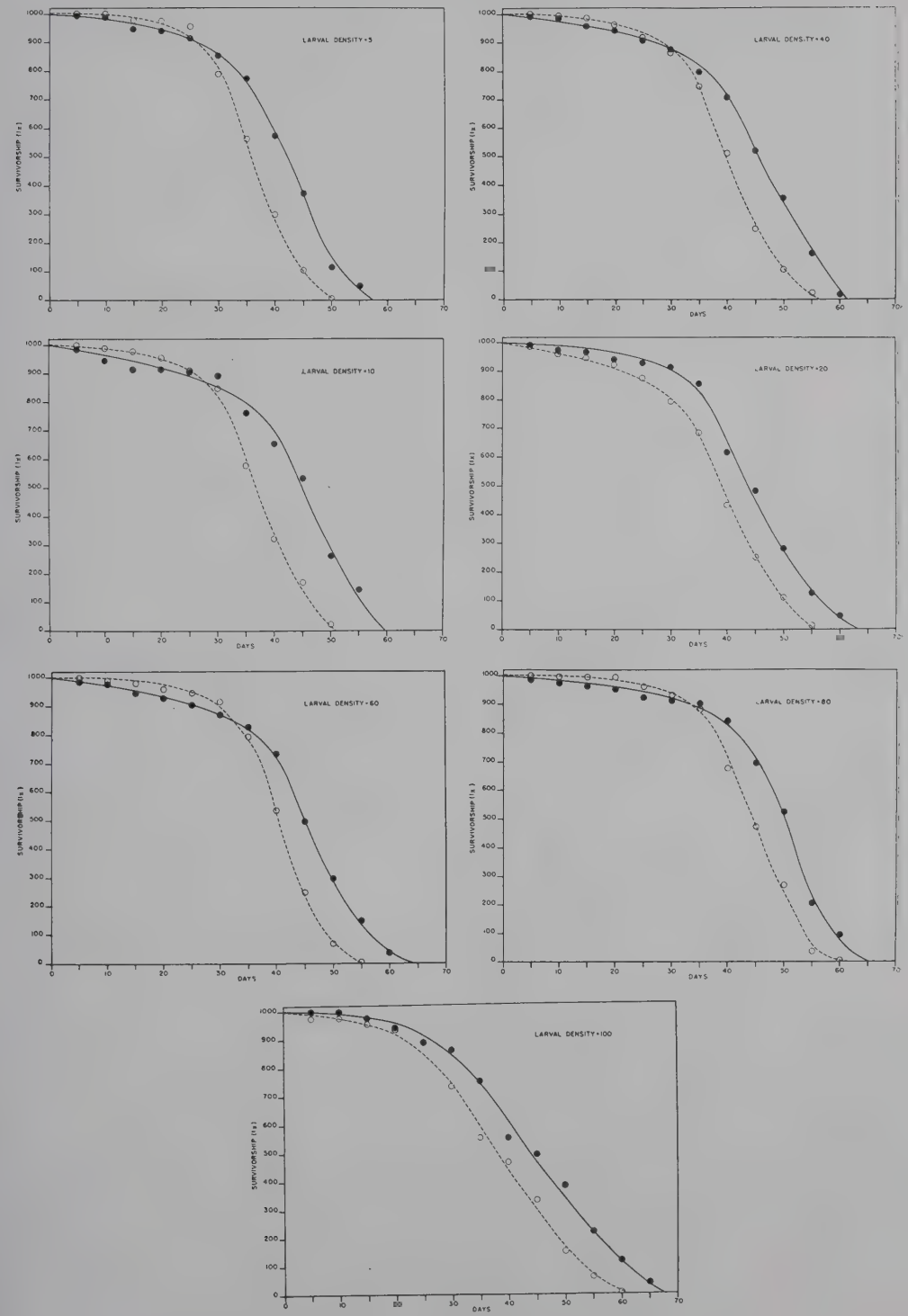

FIG. 2 a-g. Survivorship of adult *D. melanogaster*. reared at larval densities of 5, 10, 20, 40, 60, 80 and 100 per vial. Males, dots; females, circles.

TABLE IIa. Life table for adult *Drosophila melanogaster* raised at a larval density of 5 per vial

	MALES (n=155)				FEMALES (n=140)			
Days	l_x	d_x	$1000q_x$	e_x	l_x	d_x	$1000q_x$	e_x
0	1000	6	6.00	40.14	1000	0	.....	35.90
5	994	7	7.04	35.38	1000	0	.....	30.90
10	987	39	39.51	30.60	1000	21	21.00	25.90
15	948	6	6.33	26.76	979	0	.....	21.40
20	942	26	27.60	21.92	979	22	22.47	16.40
25	916	64	69.87	17.42	957	171	178.68	11.72
30	852	78	91.55	13.59	786	222	282.44	8.72
35	774	200	258.40	9.71	564	264	468.08	6.17
40	574	200	348.43	7.22	300	193	643.33	4.40
45	374	258	689.84	4.74	107	100	934.58	2.82
50	116	64	551.72	4.74	7	7	.....	2.50
55	52	52	.....	2.50				

TABLE IIb. Life table for adult *Drosophila melanogaster* raised at a larval density of 10 per vial

	MALES (n=130)				FEMALES (n=93)			
Days	l_x	d_x	$1000q_x$	e_x	l_x	d_x	$1000q_x$	e_x
0	1000	15	15.00	42.12	1000	0	.....	36.43
5	985	39	39.59	37.72	1000	11	11.00	31.43
10	946	31	32.77	34.17	989	11	11.12	26.75
15	915	0	.....	30.24	978	21	21.47	22.02
20	915	7	7.65	25.24	957	43	44.93	17.45
25	908	16	17.62	20.42	914	64	70.02	13.16
30	892	130	145.74	15.74	850	269	316.47	8.96
35	762	108	141.73	13.00	581	258	444.06	6.95
40	654	116	177.37	9.73	323	151	467.49	5.50
45	538	276	513.01	6.29	172	150	872.09	3.14
50	262	116	442.75	5.28	22	22	.....	2.50
55	146	146	.....	2.50				

TABLE IIc. Life table for adult *Drosophila melanogaster* raised at a larval density of 20 per vial

	MALES (n=270)				FEMALES (n=275)			
Days	l_x	d_x	$1000q_x$	e_x	l_x	d_x	$1000q_x$	e_x
0	1000	7	7.00	43.20	1000	14	14.00	37.46
5	993	15	15.11	38.48	986	26	26.37	32.96
10	978	11	11.25	34.04	960	11	11.46	28.78
15	967	26	26.89	29.39	949	25	26.34	24.09
20	941	11	11.69	25.14	924	48	51.95	19.68
25	930	12	12.90	20.40	876	80	91.32	15.62
30	918	59	64.27	15.64	796	112	140.70	11.94
35	859	244	284.05	11.54	684	248	362.57	8.48
40	615	133	216.26	10.12	436	185	424.31	6.88
45	482	200	414.94	7.23	251	138	549.80	5.11
50	282	156	553.19	5.58	113	95	840.71	3.30
55	126	78	619.05	4.40	18	18	.....	2.50
60	48	48	.....	2.50				

TABLE IId. Life table for adult *Drosophila melanogaster* raised at a larval density of 40 per vial

	MALES (n=219)				FEMALES (n=230)			
Days	l_x	d_x	$1000q_x$	e_x	l_x	d_x	$1000q_x$	e_x
0	1000	9	9.00	43.62	1000	0	.....	39.28
5	991	5	5.04	39.00	1000	4	4.00	34.28
10	986	27	27.38	34.18	996	9	9.04	29.41
15	959	18	18.77	29.78	987	26	26.34	24.66
20	941	32	34.01	25.60	961	44	45.79	20.26
25	909	32	35.20	21.41	917	56	61.07	16.11
30	877	78	88.94	17.10	861	113	131.24	12.00
35	799	91	113.89	14.52	748	235	314.17	8.43
40	708	188	265.54	9.94	513	265	516.57	6.14
45	520	164	315.38	7.64	248	144	580.64	5.04
50	356	196	550.56	5.00	104	82	788.46	3.56
55	160	142	887.50	3.06	22	22	.....	2.50
60	18	18	.....	2.50				

TABLE IIe. Life table for adult *Drosophila melanogaster* raised at a larval density of 60 per vial

	MALES (n=185)				FEMALES (n=150)			
Days	l_x	d_x	$1000q_x$	e_x	l_x	d_x	$1000q_x$	e_x
0	1000	16	16.00	43.26	1000	0	.....	39.66
5	984	6	6.10	38.92	1000	13	13.00	34.66
10	978	32	32.72	34.14	987	7	7.09	30.09
15	946	16	16.91	30.21	980	20	20.41	25.28
20	930	27	29.03	25.69	960	13	13.54	20.76
25	903	33	36.54	21.38	947	34	35.90	16.01
30	870	43	49.42	17.10	913	120	131.43	11.52
35	827	92	111.24	12.86	793	260	327.87	7.88
40	735	238	323.81	9.16	533	286	536.58	5.50
45	497	200	402.41	7.34	247	180	728.74	3.98
50	297	151	508.42	5.60	67	61	910.45	2.95
55	146	108	739.73	3.80	6	6	.....	2.50
60	38	38	.....	2.50				

TABLE IIf. Life table for adult *Drosophila melanogaster* raised at a larval density of 80 per vial

	MALES (n=195)				FEMALES (n=205)			
Days	l_x	d_x	$1000q_x$	e_x	l_x	d_x	$1000q_x$	e_x
0	1000	15	15.00	47.34	1000	0	.....	43.62
5	985	11	11.17	43.03	1000	5	5.00	38.62
10	974	10	10.27	38.48	995	0	.....	31.30
15	964	10	10.37	33.86	995	0	.....	28.80
20	954	31	32.50	29.19	995	34	34.17	23.80
25	923	10	10.83	25.08	961	29	30.18	19.56
30	913	10	10.95	20.33	932	49	52.58	15.08
35	903	62	68.66	15.53	883	205	232.16	10.78
50	841	144	171.22	11.49	678	205	302.36	8.29
55	697	184	263.99	8.34	473	205	433.40	5.80
60	513	308	600.39	5.44	268	229	854.48	3.32
65	205	108	526.83	4.86	39	34	871.79	3.14
70	97	97	.....	2.50	5	5	.....	2.50

TABLE IIg. Life table for adult *Drosophila melanogaster* raised at a larval density of 100 per vial

	MALES (n=136)				FEMALES (n=45)			
Days	l_x	d_x	$1000q_x$	e_x	l_x	d_x	$1000q_x$	e_x
0	1000	0	.....	43.63	1000	22	22.00	37.60
5	1000	0	.....	38.63	978	0	.....	33.40
10	1000	22	22.00	33.63	978	22	22.49	28.40
15	978	37	37.83	29.33	956	23	24.06	23.99
20	941	51	54.20	25.38	933	44	47.16	19.52
25	890	30	33.71	21.70	889	156	175.48	15.36
30	860	110	127.91	17.36	733	200	272.85	13.10
35	750	198	264.00	14.54	533	66	123.83	12.08
40	552	59	106.88	13.87	467	134	286.94	8.43
45	493	111	225.15	10.23	333	177	531.53	5.82
50	382	162	424.08	7.48	156	94	602.56	4.58
55	220	100	454.54	6.14	62	59	951.61	2.74
60	120	80	666.67	4.16	3	3	.....	2.50
65	40	40	.....	2.50				

The relationship between larval density and expectation of life at the beginning of each experiment is shown in Figure 3, and the relationship between adult body weight and expectation of life at the beginning of the experiment is shown in Figure 4. These data show a tendency toward greater longevity with increased larval density and decreased body size, although the relationship in each case is non-linear and the 100-per-vial population is an exception. There is an obvious need for further replication at the 100-per-vial density and perhaps higher densities to test the possibility of a decreased longevity with severe crowding. In general however, there is a fairly consistent trend toward greater longevity with decreased body weight, the form of the survivorship curves is similar, and an increase in maximum longevity among the longest-lived members of the population corresponds with an increase in expectation of life for the total population (Table II, Fig. 2).

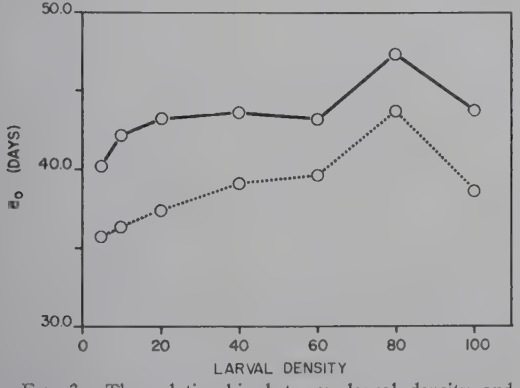

FIG. 3. The relationship between larval density and expectation of life at the beginning of each experiment (e_0) for adult *D. melanogaster*. Males, solid line; females, broken line.

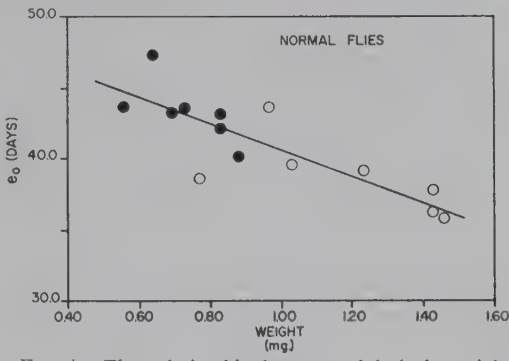

FIG. 4. The relationship between adult body weight and expectation of life at the beginning of each experiment for normal adult *D. melanogaster*. Males, dots; females, circles.

Another feature of these data is the greater maximum longevity and expectation of life of the male flies, in spite of a slightly higher mortality rate during the early intervals (Table II, Fig. 2).

TABLE III. Survivorship of starved flies raised at larval densities of 20 (culture A) and 80 (culture B) per vial

	A				B			
	Males		Females		Males		Females	
Larval density:	20		20		80		80	
Mean body wt. (mg):	0.86		1.39		0.65		0.82	
n=	65		70		80		80	
Hours	l_x	e_x	l_x	e_x	l_x	e_x	l_x	e_x
0	1000	15.53	1000	22.99	1000	12.18	1000	14.93
1								
2								
3								
4					988	8.30	1000	10.93
5								
6								
7								
8					962	4.47	962	7.28
9								
10								
11								
12								
13								
14								
15								
16	667	3.29	925	8.20	75	2.07	400	3.89
17								
18					25	2.20	238	3.85
19	317	2.26	800	6.25				
20					12	1.50	162	3.19
21	167	1.39	700	5.00				
22								
23	33	1.00	550	4.09			100	1.24
24								
25			400	3.25			12	1.00
26								
27			300	2.00				
28								
29			150	1.00				
30								

This was a consistent relationship in each population.

According to Pearl (1922) and Pearl & Parker (1924), female flies should live longer than males and large flies should live longer than small ones, if longevity is a function of size and available energy reserves. In view of the contradiction offered by the present data, it seemed advisable to repeat the experiments of Pearl & Parker (1924) with starved flies, using adults reared from larval cultures of 20 and 80 per vial since these densities provide a clear separation in adult body size and the results from populations raised at these densities were measurably different in the present study. Adult flies from populations reared at these two densities were collected within a half-hour after emergence and placed 5 per vial in eight-dram vials. They were given neither food nor water throughout their duration of life and since adult feeding does not begin until a few hours after emergence, they were unfed from the time of pupation. The vials were kept at 25°C and 75-80% R.H. and the number alive in each vial recorded periodically. The results of this experiment are shown in Table III and illustrated as the relationship between adult body weight and expectation of life (e_o) in Figure 5. Starved flies showed longevity characteristics which were opposite to those observed with normal flies.

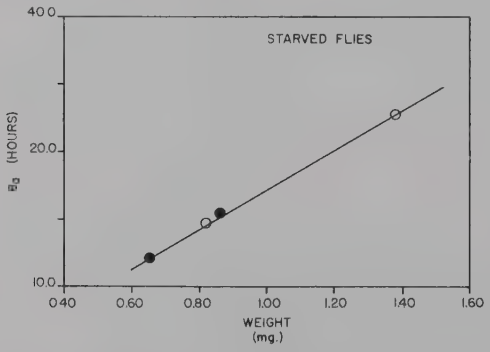

FIG. 5. The relationship between adult body weight and expectation of life at the beginning of each experiment for starved adult *D. melanogaster*. Males, dots; females, circles.

DISCUSSION

These results show that the lengevity characteristics of starved flies do not represent "inherent vitality" in terms of the longevity that is expressed when food is adequate, and the physiological longevity concept, as defined by Pearl (1922) for *Drosophila,* is therefore not applicable to normal situations. In the absence of food, body size and total stored energy reserves confer a definite advantage toward greater longevity, but in the presence of an external food supply longevity depends upon the organism's ability to utilize such resources, and this ability does not seem to be a function of body size alone.

Glycogen forms dense deposits in the cells of the fat body and in the haltere knobs, and is distributed throughout the flight muscles as minute granules in the network of sarcoplasm between the fibrils and sarcosomes of an adult *Drosophila* (Wigglesworth 1949), whereas visible fat deposits are found only in the fat body and mid-gut cells. In a newly emerged imago the "larval fat body" is still evident and fills a large part of the abdomen, but the only demonstrable glycogen is confined to traces in the halteres. Consequently, a *Drosophila* imago is not physiologically mature until about 4 or 5 days after emergence, when the larval fat body has disappeared and the adult fat body has become enlarged with accumulated glycogen deposits.

Wigglesworth (1949) has also shown histologically that glycogen and fat are consumed concurrently during starvation in adult *Drosophila;* at the time of death, glycogen has disappeared except for traces in the thoracic muscles and only minute droplets of fat remain in the fat body. During the normal exercise of flight, however, there is an R.Q. of unity, indicating that carbohydrates are being utilized, and glycogen is reduced in all deposits with no apparent reduction in fat in an insect flown to exhaustion (Chadwick & Gilmour 1940). Williams (1941) offers the view, at least partially substantiated by Wigglesworth's observations, that flight fatigue is to be explained in terms of the disappearance of carbohydrates, and since the metabolic events of insect flight are a more natural series of phenomena than those occurring during artificial starvation, we must conclude that longevity experiments with starved *Drosophila,* particularly with newly emerged flies, do not reflect normal physiological conditions.

Since the present experiments did not include direct measurements of metabolic rates, they offer no quantitative evaluation of the effects of body activity. Observations during the experiments indicated, however, that activity varies with age, size, and sex and that small flies tend to be more active than large flies. During the first few days of an experiment the flies spent most of their time feeding and were otherwise relatively inactive, but after about a week they flew vigorously when disturbed and sustained this response until the population began to decline in numbers and an apparent "senescence" had begun. A few days before death they became extremely sluggish and could seldom be aroused to flight. These obser-

vations are roughly parellel to the experimental data of Wigglesworth (1949) and Williams, Barness & Sawyer (1943). The average duration of flight as well as the speed of recovery from flight exhaustion is greatest in *Drosophila* several days after emergence, but declines steadily thereafter, so that there appears to be a period of maturation during which the capacity for sustained flight increases, followed by a longer period of aging during which the capacity for sustained flight declines. These periods of changing flight capacity reflect physiological adjustments that may in turn represent variations in the aging process. Crozier & Enzmann (1937) experimented with the resistance of *Drosophila* to alcohol vapors and concluded that there are periodic fluctuations in the speed of general metabolic events during duration of life, marking the limits of what they termed "metabolic instars." Thus, the process of aging appears to be discontinuous and cannot be characterized as a gradual depletion of energy reserves.

The results of the present study suggest the tentative hypothesis that increased metabolic activity brought about through larval crowding and decreased adult body size may have the effect of prolonging, rather than shortening, duration of life. In view of the nature of *Drosophila* metabolism, such a mechanism might be one in which an increased metabolic rate aids in the mobilization of glycogen and provides for more prompt recovery from carbohydrate depletion.

Summary

1. The effects of larval crowding on the size and longevity of adult *Drosophila melanogaster* were studied and compared with the longevity relationships established by Pearl (1922) for starved flies.

2. With adult nutrition adequate and with the adults kept under uncrowded conditions during the duration of their life, larval crowding and corresponding decreases in adult body size tended to increase expectation of life and maximum longevity. There was a tendency for small flies to live longer than large flies, and for males to have a greater expectation of life than females.

3. In the absence of food, the above relationships are reversed; females live longer than males and large flies live longer than small flies.

4. These results show that the longevity performance of starved flies is not a reliable index of "ecological longevity" and it cannot be assumed that duration of life is a simple function of the time required to transform limited amounts of energy.

5. It is suggested that increased activity and metabolic rate may increase longevity under certain conditions, possibly through more efficient mobilization of glycogen and more prompt recovery from carbohydrate depletion.

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REACTIONS OF AMERICAN AND FRENCH SPECIES OF *CORVUS* AND *LARUS* TO RECORDED COMMUNICATION SIGNALS TESTED RECIPROCALLY

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In 1953, it was found that starlings could be driven from objectionable tree roosts by broadcasting to them the recorded distress call of the species (Frings and Jumber 1954). This led to further studies in the United States on the possibility of influencing the behavior of pest birds with recorded communication signals and through this to fundamental studies on acoustical behavior of these species. Similar studies were made simultaneously on pest birds in France. In 1954, 1955 and 1956, both the European workers and the American workers studied crows resident in their countries. The American workers studied also Herring Gulls and found ways to influence the behavior of these birds with broadcasts of recorded communication signals. These successes led the two laboratories involved to decide upon an exchange of recordings for the purpose of testing the possible intraspecific and interspecific semantic values of the calls. This paper, which is Paper No. 2101 in the journal series of the Pennsylvania Agricultural Experiment Station, reports the results of these tests to date.

EXPERIMENTS ON CROWS

Tests in the United States

The only crow studied by the American investigators in the U. S. is *Corvus brachyrhynchos brachyrhynchos* (Eastern Crow). The species is the common crow generally distributed over the U. S. The subspecies studied is found in the eastern states northward from the Gulf states and northern Texas to Newfoundland and northern Manitoba (Bent 1946). Three other subspecies are recognized (Bent 1946): *C. b. paulus* (Southern Crow), in the southeastern part of the U. S.; *C. b. pascuus* (Florida Crow), in the Florida peninsula; and *C. b. hesperis* (Western Crow), in the western part of the range. A smaller species, *Corvus ossifragus* (Fish Crow), is also found in the eastern U. S., mostly in the southern states, occurring as far north as southern Massachusetts in the summer and not as far north in the winter. A third species, *Corvus caurinus* (Northwestern Crow) occurs in the extreme northwestern U. S. and thence northward to Alaska.

For this study, the calls of the Eastern Crow were recorded in the field on tape (at 7½ in./sec) with either a Pentron, Model 9T-3C, or an Ampex, Model 350P, tape recorder. The behavior of the birds during the recording was observed to determine the possible significance of the calls. Copies of the recordings were made on continuous loop tape cartridges played by a special player (Message Repeater) through either a special amplifier designed for use with this player or a Stromberg-Carlson, Model AU-42, amplifier and University, Model PA 30, speakers. The Message Repeater and special amplifier were kindly supplied for these tests by the manufacturer, Mohawk Business Machines Corporation of Brooklyn, New York.

Tests with the calls were carried out during the daytime only. With this mobile broadcasting equipment in an automobile, some suitable location was selected and the sounds were broadcast at relatively high intensities—about 120 db at 1 m from the speaker. Ordinarily no crows were in sight at the start of the tests; therefore attractive or supposedly attractive calls were tested first. The recorded sequences were of either one or three minutes' duration, and they were repeated to give totals of six, nine or ten minutes.

No attempt was made to test all the calls of the Eastern Crow. Four signals were selected for testing, based on the possibility that these might have greatest utility in influencing the behavior of the birds: (1) the assembly call, given when crows sight an owl or cat; (2) the alarm call, given by a single crow which has sighted danger; (3) ordinary cawing, given by all individuals at times; and (4) begging cries of young nestlings. Attempts were made to capture normal adults for possible distress calls, but these proved fruitless; injured adults did not give distress calls. It is impossible to decide the relationship of these calls to those reported earlier in the literature (Bent 1946) by syllables. Recordings of the calls studied here are on record with the International Collection of Animal Phonography (Frings and Frings 1956).

During the summer of 1955 (July 5-Sept. 4), tests of these calls were made on Mt. Desert Island, Maine. The assembly call proved to be

strikingly attractive to the crows. In 27 out of 30 tests, groups of crows numbering 2-30 came to the sound source within 1-5 minutes. The alarm call proved to be repellent, even at low intensities. Tests with this could be made only on crows already attracted or where they could be seen. In about 20 tests, it dispersed the crows with only one or two repetitions of the call, about 5-10 seconds. The other calls had no observable effects on the movements of the birds. These results have been reported in detail elsewhere (Frings and Frings 1957).

During the winter of 1955-56 (Oct. 20-March 5), tests were made near State College, Pennsylvania, with essentially the same results. In 30 tests each, cawing and the sounds of nestlings proved to have no observable effects on the movements of the birds. In about 50 tests, the assembly call failed only six times to attract groups of 5-200 crows within 1-6 minutes. By using a stuffed Great Horned Owl (*Bubo virginianus*) as a visual reinforcement, these groups could be induced to approach the sound source and to remain nearby for long times. In about 30 tests, the alarm call proved to be repellent, except in the cases where the stuffed owl was present. Unfortunately, conditions beyond our control prevented tests of the alarm call on birds in large winter roosts.

These results may be summarized, therefore, as follows. The assembly call of the Eastern Crow, which is emitted by groups of crows which have sighted a cat or an owl, when recorded and broadcast to the birds in the field, is strongly attractive, bringing the birds in quite close to the sound source. When they have approached to a distance from which they can clearly see the sound source, they settle on some vantage point to observe. Only by visual reinforcement, with a stuffed owl for instance, can the birds be induced to approach quite close to the speaker or a person and to remain nearby. The alarm call, which is emitted by an individual crow on sighting danger, is repellent even at low intensities; thus mere intensity of sound is not the repellent factor. In many cases recordings of the calls of other species—gulls, ducks, wild turkeys, etc.—were broadcast without having any observable effects on the movements of crows. Likewise, the crow calls, except in a few cases, had no influence on the behavior of other birds in the neighborhood. These sounds are thus specific signals, and are used by crows for communication.

Tests in France

Three species of the genus *Corvus* are found in France, and during the winter intermingle in large flocks: *Corvus monedula* (in English, Jackdaw; in French, Choucas), *C. frugilegus* (Rook; Freux), and *C. corone corone* (Carrion Crow; Corneille noire). The social behavior of the Carrion Crow is much like that of the American Eastern Crow, but the social behavior of the other two species is more nearly like that of the American *Sturnus vulgaris* (Starling). In winter, the French species gather in large numbers for roosting at night and feed in flocks numbering from ten to hundreds during the day. These frequently include representatives of all three species, with *C. frugilegus* usually predominant.

The call with which the most detailed studies were made was the distress call of *C. monedula,* for the effects of broadcasting this call were very striking. This was selected for study from among a number of calls which were tested and found to have less effect or no observable effects on the flocks. The distress call was recorded on tape as emitted by individuals which were held by the legs or caught by a falcon, and then either played back from a disk record or from a tape cartridge by the Message Repeater through an amplifier and speaker mounted on a truck. The intensity was such as to give the sound a range of 1,500-2,500 m. Usually the distance from the truck to the flocks was 50-2,000 m. The flocks were feeding in fields and were always in sight at the beginning of the tests, unlike the situation in the U. S. The sound was emitted for about 20 seconds and then turned off. In about two minutes, there was another emission, and the sound was repeated thus 2-4 times. Most of the tests were made near Paris from November to March, 1954-55 and 1955-56.

Reactions to the sound were classified into three major and some minor categories. When the birds flew up from the ground, circled to gain altitude and approached the speaker, the reaction was called positive phonotaxis. If the sound was kept on, the birds circled near the speaker, generally vocalizing, and dispersed individually. If the sound was turned off, the birds circled higher and higher and disappeared as a group. If, after the birds started to leave, the sound was re-emitted, they returned to the source. Positive phonotaxis was divided into five classes, designated as follows: +++, if the reaction was immediate and direct, ++, if the reaction was good but not immediate, +, if only part of the flock was attracted, +—, if some were attracted while others flew away, and +o, if some approached the sound source while others remained on the ground. When the birds flew up from the ground and then away from or at some angle to the sound source, the reaction was called negative phonotaxis. Two classes were recognized: —, if the birds

all flew thus, and —o, if only part flew thus while the others remained on the ground. In some cases there was no apparent reaction to the sound, and these were designated as negative, symbolized by o.

The general methods for recording and projecting the calls of the birds were thus similar to those used by the American workers, but the observations were made somewhat differently. In the tests in the U. S., usually no birds were in sight at the start and counts were made of the birds which were in sight at 30 second intervals during the broadcasting of the sound. In France, the birds were in sight at the beginning of the tests, and the reactions of the flocks were thus susceptible of classification into reaction types. Further, the crows in the U. S. were in much smaller groups and much more dispersed than those in France.

The results of the tests in France are summarized in Table I, where the symbols are those defined above. It is clear that the distress call of *C. monedula* usually has great effect on the movement of flocks of the three species. In about 75% of the cases it serves to disperse the flocks, either directly or through circling flight which brings the birds closer to the sound source at first and later away.

TABLE I. Results of tests with the recorded distress call of *C. monedula* and the recorded assembly call of *C. brachyrhynchos* when broadcast to feeding flocks of French *Corvus* spp. The symbols are explained in the text; those with +, indicate positive phonotaxis, with —, negative phonotaxis, and with o, no reaction

Type of Reaction	Species Whose Call Was Broadcast: *C. monedula* No. of React.	*C. monedula* % of React.	*C. brachyrhynchos* No. of React.	*C. brachyrhynchos* % of React.
+++, ++ or +.....	20	40%	16	31%
+— or +o..	8	16%	12	23%
— or —o....	10	20%	6	11%
o.....	12	24%	18	35%

Tests were also made at night with the distress call of *C. monedula* at a roosting place for about 2000 of these birds near Paris (Busnel *et al.* 1955). With four minutes of sound at 10:30 P.M., the birds rose from the roost, circled in the air and left, not to return until six nights later. In seven similar tests at other places they stayed away from the roosts for 3-30 days. The distress call thus has effects with roosting corvines similar to the effects found for the distress call of the Starling in the U. S. (Frings and Jumber 1954).

Tests with Exchanged Recorded Calls

The investigators in the U. S. received from the French investigators, in the spring of 1955, the following calls of French birds: distress calls of *C. monedula, C. frugilegus,* and *C. corone,* and calls of nestling *C. frugilegus.* These were tested in the summer of 1955 at Mt. Desert Island, Maine, and in the winter of 1955-56 near State College, Pennsylvania, during the tests with the native crow calls. With the distress calls of all three species (20 tests with each) no observable results were obtained. During the summer, with the calls of young *C. frugilegus,* no observable reactions were obtained, but during the winter, some attractive properties appeared. In ten tests at this time, seven resulted in approaches to the sound source by a few crows: in two cases 2 crows, in three cases 3 crows, in one case 4 crows, and in one case 5 crows. These flew over slowly, as if investigating, and did not remain for more than one to two minutes at the most. Thus there was some attraction but not nearly so much as with the native call, and the reaction seemed more like curiosity than the purposive assembling elicited by the assembly call of the Eastern Crow itself.

The investigators in France received from the U. S. the following calls of the Eastern Crow: assembly call, alarm call, cawing, and the cries of nestlings. These were tested, along with the distress call of *C. monedula,* near Paris in the winter of 1955-56. The alarm call, cawing and cries of nestlings proved ineffective in eliciting any observable reactions in flocks of the three species of corvines. The reactions to the assembly call, however, were much like those to the distress call of *C. monedula,* as shown in Table I. While no statistically significant differences between the reaction to the two calls were found, the intensity of response to the American call seemed to be less than to the native call. With the French call, the birds circled near the speaker and dispersed one by one if the sound persisted. With the American crow call, the birds flew toward the speaker, did not circle, and dispersed in groups.

By April, 1956, therefore, it seemed that the Eastern Crow in the U. S. reacted very specifically to its own calls, the French calls arousing only slight reactions. On the other hand, the French birds reacted to both their own distress calls and to the assembly call of the U. S. crow, thus seeming to be less specific in their reactive potentialities. At this time, the French investigators came to the U. S. with a new recording of the distress call of *C. monedula,* and tests were made during June, 1956, with somewhat different results.

The first tests were made in Pennsylvania, near State College, on June 3-5. In five of the first six tests, using paired trials with the two calls, the French call had effects almost exactly like those of the assembly call of the Eastern Crow. The earlier results had been so decidely negative that it seemed possible that the new recording might be different from the older one, even though to the human ear they sounded much alike. Accordingly, four tests were made with the older recording, with the same results as with the new recording. Thus there was a real difference between the reactions at this time and those during the previous summer and winter.

The next hypothesis was that the extreme hunting pressure on the crows in Pennsylvania during the breeding and planting season caused them to become reactive to almost any unusual sounds. Accordingly, a series of recorded sounds (duck vocalizations, mosquito wing sounds, etc.) were broadcast. There were no observable reactions to these, even when the crows were visible during the tests. It would seem, therefore, that mere unusual sounds were not responsible.

The difference in reactions seemed thus to be related either to seasonal or geographic factors, for the summer tests of 1955 were conducted in Maine. Accordingly, tests exactly like those in Pennsylvania, using paired trials of the assembly call of the Eastern Crow and the distress call of *C. monedula,* were made at Mt. Desert Island, Maine on June 12-14.

In 14 tests, no reaction was obtained to the distress call of *C. monedula,* just as during the previous summer, while the usual high reactivity to the assembly call was found. In fact, the difference in the reaction of these crows to the French call was so striking that it seemed impossible that we could be testing the same call at all, while the reactions to the American call were exactly similar in Pennsylvania and Maine. Thus, there is a true difference in reaction to the French call between crows in central Pennsylvania and those in northeastern Maine, even though these are of the same subspecies.

Experiments on Herring Gulls

In the summer of 1954, the investigators in the U. S. studied the reactions of *Larus argentatus* (Herring Gull) to broadcasts of recorded communication signals of this species (Frings *et al.* 1955a, 1955b). Briefly, four calls were clearly separable in origin and effects at feeding areas: a food-finding call, emitted by gulls on sighting food, which proved to be quite attractive to other gulls; an alarm call, emitted by gulls sighting danger, which proved to be strikingly repellent; and the mew call and trumpeting, both of great importance in breeding colonies but without clearly definable effects among feeding gulls.

Copies of these calls were sent to the French investigators for broadcasting to colonies of *Larus argentatus* (in English, Herring Gull; in French, Goëland argenté) and *L. ridibundus* (Black-headed Gull; Mouette Rieuse). The former is, of course, the same species as that in the U. S. The tests were made during the winter of 1955-56 with continental flocks of gulls. Since the calls of Herring Gulls had the same effects in the U. S. with *Larus marinus* (Great Black-backed Gull) and *L. atricilla* (Laughing Gull), it seemed reasonable to expect that they would have similar effects in France, at least with *L. argentatus.*

The results were quite surprising—the calls were totally lacking in observable effects on the French gulls. This was later checked by Mr. G. Jansen of Rotterdam, Holland, who tried to use the recorded alarm call of the U. S. Herring Gull to drive gulls from an airport near Rotterdam without having any observable movement of the gulls, even when the call was broadcast from very short distances. In the U. S., flight from the sound source was achieved at distances up to 2 miles, with the intensity only about 95 db at 1 m from the speaker. Since recorded samples of the calls of European Herring Gulls have not yet been received for testing in the U. S., the explanation for this discrepancy remains unknown, but the results are given as an illustration of some possible subspecific differentiation in understanding of the signals. The tests in Europe were made during the winter and early spring, while those in the U. S. were made during the summer; the differences may thus be related to the time of year. Only further tests can decide the question.

Discussion

An acoustical note should be made on these tests. With field equipment, fidelity of reproduction is at times much reduced, and to the human ear at least the sounds broadcast to the birds are distorted or partially masked with background noise or hum. Yet they seem to be "understood" quite readily by the birds. It may be that the physical parameters determining the effectiveness for birds are not the same as those determining fidelity for the human ear. The similarity of the ears of birds and mammals, however, makes this seem not too likely. More likely, these communication signals are capable of being distinguished by the birds over high levels of background interference. This would be particularly the case for warning sounds, such as a distress call or an assembly call like that of the Eastern Crow.

What hypotheses might one set up to explain the results obtained? It is obvious that, in the species of *Corvus* we tested, three different levels of specificity in reactions to communication signals are represented—the Eastern Crow in Maine during the summer and in Pennsylvania during the winter seems to be very specific in its reactions, this species in Pennsylvania during the summer seems to be less specific, and the three French species seem to be least specific of those tested. The difference between the behavior of the American *Corvus brachyrhynchos* and the French species of *Corvus* may be related to the fact that the American crows are usually found in flocks consisting of only one species, or in the southern part of the range two species, while the French birds associate interspecifically during the winter. Thus the French corvines might learn to react to more generalized features of warning sounds than their American congeners. As substantiation of this, the French species were found to react to the distress call when it was cut into sections or played backwards.

There are two important differences between the Eastern Crows in Maine and in Pennsylvania during the early summer. First, the crows in Pennsylvania are much more severely hunted than those in Maine, at least where these tests were made. It is conceivable that this might make them much more reactive to all warning sounds in Pennsylvania at this time. The exact similarity in reactions to the assembly call, however, lends little support to this idea. The second difference is that the crows living in Maine in the summer move southward for the winter to southern New England and Pennsylvania, while those in Pennsylvania move southward into the southern states (Bent 1946). This means that the crows tested during the winter in Pennsylvania are from a population equivalent to that tested during the summer in Maine. Further, they represent individuals which mingle generally only with other members of the same species. But the crows which move southward from Pennsylvania in the winter mingle with the different southern subspecies and, possibly of more importance, with the Fish Crow. This is reported as having a hoarser sounding voice than that of the Eastern Crow (Bent 1946). The distress call of *C. monedula* is much more hoarse in sound than the call of the Eastern Crow. Is it possible that the crows which spend the summer in Pennsylvania, having just arrived in June from these associations, have learned to react to a wider gamut of warning sounds, and thus have become reactive to the coarser call of *C. monedula*? We believe that this is, at present, the most reasonable assumption.

This idea is supported by the following observations made by the American investigators and reported here for the first time. In Maine, two species of gulls are found together—*L. argeniatus* and *L. marinus*—with the former by far in the majority. The latter always react quite typically to the calls of the former, but usually not the reverse. Eastern Crows also are often found feeding with Herring Gulls in Maine, and there is considerable cross-reactivity in calls, depending upon the population structure. It is interesting to note that, in a few cases, Herring Gulls in Maine responded similarly to the distress call of the French crow by flying in circles over the sound source. In tests with the distress call of *Sturnus vulgaris* (Starling), we have found that, with mixed roosts including *Molothus ater* (Brown-headed Cowbirds), *Quiscalus quiscula* (Common Grackles), or *Progne subis* (Purple Martins), the species other than Starlings will leave with the Starlings if they form a small fraction of the roosting birds, but may not if they form a large fraction. Thus it seems that minority groups flocking with other species may learn to react to the signals of the majority as to their own, but not necessarily the reverse. It has been well known to most naturalists since Aristotle that alarm calls of passerine birds which have sighted a hawk or cat attract individuals of other species.

The meaning of the subspecificity in the Herring Gull remains to be determined. A report from Europe suggests that the European Starling may also fail to react to the recorded distress call of its American conspecies, and that the European Starling may have a different signal.

We feel that all these observations suggest that birds develop basic communication signals within each species having features in common with those of related species, but sometimes with regional variations. In cases in which individuals are exposed only to the signals of their own group, they may become quite specific in reactions. In cases where they mingle with other populations of their own species or with populations of related or non-related species, they may learn to respond to the signals of these.

These are probably behavioral isolating and hybridizing mechanisms—the substructure of evolutionary change, as Blair (1955a, 1955b, 1956) has studied in Amphibia and Fulton (1933, 1937) in crickets. For the birds, much work is needed before we shall be in a position to formulate even provisional theories. Studies should be made with different geographic and season populations of the same species and with reactions of birds to calls of related or distant species as functions of population structure. Only when the full "vocabu-

laries" of many species are tested over wide geographic areas and with contiguous and distant populations of the same or related species will we be ready to develop theories relating the ecological, evolutionary, acoustical, and behavioral parameters of these behavior patterns.

From the standopint of possible practical utility in controlling the movements of economically important species, these results emphasize the need for careful studies on habits of birds if attempts to influence their behavior are to be made successfully. It may not be sufficient merely to broadcast recorded calls to birds to get specific results. Only critical observations of behavior as related to geographic distribution, seasonal movements and ecological relations can give the basic information needed for effective control measures.

Summary

In the U. S., Eastern Crows (*C. b. brachyrhynchos*) emit an assembly call on sighting an owl or cat which, when recorded and broadcast to crows in the field, causes aggregation near the sound source. An alarm call, emitted when the crows sight danger, when broadcast similarly, causes the birds to fly away.

In France, three species of *Corvus* (*C. monedula, C. frugilegus,* and *C. c. corone*) roost and feed together during the winter. Broadcasts of recorded distress calls, emitted when the birds are restrained or injured, cause the birds to approach the sound source at first and afterward to disperse. The distress call of *C. monedula* proved to be most effective. When broadcast at night near roosts, the call causes the birds to desert the roosts.

Using exchanged recordings, the distress calls of the French corvines were broadcast to crows in the U. S. There were no observable reactions by the birds in Maine during the summer and Pennsylvania during the winter. In early summer, in Pennsylvania however, the distress call of *C. monedula* induced crows to approach the sound source. In France, the three species did not respond to the recorded alarm call of the American species, but reacted to the assembly call of the American crow as they did to the distress calls of the French birds.

In the U. S., the Herring Gull (*L. argentatus*) responds to its own food-finding call when recorded and broadcast, by approaching the sound source and to broadcasts of its alarm call by dispersal. In France, with the same species, the calls elicit no response.

These observations suggest that these birds develop communication signals within each species having features in common with those of related species, but sometimes with regional variations within the species. In cases in which individuals are exposed only to the signals of their own group, they may become quite specific in reaction. In cases where they mingle with other groups of their own or other species they may learn to respond to the signals of these.

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ECOLOGY OF THE POLYHEDROSES OF TENT CATERPILLARS

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INTRODUCTION

Information on the polyhedrosis diseases of the tent caterpillars has been accumulating for a number of years. Howard & Fiske (1912) cite an earlier reference (New Hampshire Agr. Exp. Station Tech. Series No. 5) to a disease similar to the polyhedrosis they were studying in the gipsy moth. They state that this reference reported the destruction of a population of tent caterpillars in 1898. Davis (1903) recorded a destructive epizootic among a population of *Malacosoma americanum* (F.) in Pennsylvania, New York, and New Jersey in 1903. Chapman and Glaser (1916) and Glaser (1927, and other reports) studied the histopathology and other aspects of polyhedrosis in *M. americanum* in considerable detail. As has been traced elsewhere (Clark and Thompson 1954), polyhedroses have been subsequently reported from most of the North American species of tent caterpillars. To date no real differences between the diseases have been reported. In field tests, the viruses causing the diseases have been collected from populations of *Malacosoma fragile* (Stretch), *Malacosoma californicum* (Pack.), *Malacosoma disstria* Hbn., or *Malacosoma contrictum* (Stretch), and freely used to initiate infections among populations of any of the other species. Such field cross-infections have been made both sympatrically and allopatrically.

To facilitate this discussion of the ecology of the polyhedroses of tent caterpillars, a brief review of other aspects of this group of insect diseases is presented. For a detailed and historical review, the reader is referred to Steinhaus (1949).

Etiology

In addition to several other infectious diseases, a good many species of Lepidoptera are known to be susceptible to the group of virus-caused diseases now called polyhedroses. The identity of the causal agents as viruses was established by G. H. Bergold in 1947. The etiology and histopathology of the diseases in this group are very similar throughout their occurrence in different species and in different families in the order Lepidoptera. Several distinct viruses are involved. The virus rods are similar morphologically, but do show size variation. Usually host susceptibility is the only certain means of identification. Bergold (1953) reviewed the known morphological, chemical, and physical properties of this group of insect viruses.

Characteristic of the polyhedroses are the protein inclusion bodies within which the virus rods are occluded. These microscopic (0.5μ to 15μ, Bergold, 1953) bodies are angular rather than round in outline, hence the term "polyhedra." The polyhedral protein is not pathogenic. When occluded within these bodies, the virus is resistant to very low temperatures, heat beyond the range occurring in the environment of the host insect, and desiccation, and retains pathogenicity for long periods. A common practice in working with the polyhedra-enclosed viruses is storage below —35° C. According to Bergold (1953), Bolle in 1907 reported the retention of infectivity of the virus of the silkworm after storage of 25 years. Steinhaus (1954b) demonstrated infectivity of the virus of the silkworm after 15 years' storage in tubes mostly at 4° C.

Pathology

The natural mode of entry of the pathogen is ingestion with the food. Infection proceeds in the nuclei of the fat, hypodermal, blood, tracheal matrix, and genital cells. The wall of the gut is the principal tissue not infected in the polyhedroses of the Lepidoptera. As the infection progresses, the newly forming polyhedra distend the nuclear membrane. Finally the nuclear and cell membranes break down and the polyhedra occluding the virus are liberated into the haemocoele. At the conclusion of the process, the body fluids carry a heavy concentration of polyhedra. As a result of infection of the hypodermal cells, the integument becomes fragile and with rupture releases this concentration of polyhedra over the site of death of the host.

In general infection is initiated only in the larval stage. Insects infected late in this period may, however, die as pupae. There is a marked increase in resistance with increasing larval age. The nature of this resistance is unknown, but it is known that older larvae can ingest large doses of virus and survive, pupate, and oviposit as adults.

This apparent resistance, or recovery from infection which may be involved, provokes an important ecological question. The exposed but surviving larvae have been considered a source of infection for the larvae of succeeding generations

by the way of contaminated eggs. Transmission of the virus in association with the egg is generally accepted. Glaser (1927) mated and obtained eggs from 10 tent caterpillar adults which had survived infection as larvae. Twenty-five larvae hatching from these eggs were reared individually under aseptic conditions. Glaser reported that 3 of the 25 larvae died of polyhedrosis and indicated his belief that the mortality rate would have been higher had the larvae been reared in a group. Clark (1955) reared *en masse* in a greenhouse larvae from egg masses collected from an area of a natural epizootic among an *M. fragile* population and reported only 15 survivors in this generation.

While transmission of the virus with the egg is accepted, the nature of the resistance to, or recovery from, infection is not at all understood. The relationship of the transmitted virus to the egg is also unclear.

The ecological significance of this phenomenon lies primarily in the quantitative aspects. The proportion of adults that survive an epizootic of a given mortality rate and transmit the virus to their progeny is completely unknown.

Ecology

Although the cause of the polyhedroses has been clarified only recently, reports of the destruction of lepidopterous populations have been common for many years. Reports of the sudden and complete collapse of populations of forest defoliators as brought about by the polyhedroses are numerous, but we do not have adequate data on the extent or change in extent of the disease prior to the year or years of almost complete mortality of the host. An important generalization, however, is that the polyhedroses frequently do not reach a peak incidence until the host insect reaches and maintains for two, three, or more years a density resulting in near-complete defoliation of the host plant. Thus, in various assessments of the economic value of the diseases in controlling pests, the statement that they become effective two or three years too late to prevent serious damage by the insect is common (Howard and Fiske 1912; Komarek and Breindl 1924; Bergold 1943; Dowden 1952). The most frequently reported sequence of events, then, is the increase of the host insect to extremely heavy densities, maintenance of these densities over a period of years, and the appearance and increase in incidence of the disease to the intensity at which the population is destroyed. It is well recognized, however, that low populations of susceptible species are relatively poorly observed, and the incidence of the polyhedroses among these populations is not known. Additionally, populations of susceptible hosts may be eliminated by other factors before the disease is known to occur.

In general terms and without substantiating data, Komarek and Breindl (1924) described their impressions of changes in incidence of the disease occurring in a population of the nun moth, *Porthetria monacha* (L.), from year to year. They believed that there was a regular increase in prevalence and a correlated increase in the proportion of mortality occurring among younger larvae as compared to the proportion of mortality occurring among the older larvae. They ascribed these changes to increased distribution and to increased virulence of the virus. Changes in the virulence of the polyhedroses viruses of insects have not been demonstrated. Clark (1955) recorded an incomplete series of observations on a polyhedrosis epizootic of *M. fragile* in California. These observations suggested a similar year-to-year shift in mortality proportion from the older to the younger larvae.

The writer is indebted to entomologists of the U. S. Forest Service for observations on the changes in mortality rate among a tent caterpillar population infesting aspen, *Populus tremuloides* Michx., near Taos, New Mexico. This population has been extremely heavy since before 1950. In 1954, forest entomologists noticed a few insects with symptoms of polyhedrosis and this diagnosis was confirmed by laboratory procedures. In 1955, the disease occurred at a noticeably higher incidence and was widely distributed throughout the area. By 1956, the disease reached the point at which polyhedrosis-killed larvae were found on nearly every tent, and the larvae of many or most tents were nearly all destroyed.

While the foregoing reports and observations suggest a regular increase in disease incidence, their meagerness and the lack of reliable data underscore the need for information before attempting to draw conclusions concerning the ecology of the diseases.

Transmission of the disease from larva to larva within a single generation is known to occur under experimental conditions (Clark 1955). As described in a foregoing section, the tissues that become infected in an individual caterpillar are such that the release of most of the newly-formed virus-occluding polyhedra appears to be into the haemocoele. These polyhedra become available to other larvae after disintegration following death. Considering the period from ingestion to death of about six to twenty or more days depending on dosage, larval age, temperatures, and perhaps physiological variables, the number of cycles of larva-to-larva transmission which end in fatal infections is probably quite limited. As Bergold

(1943) has pointed out, however, the prolonged hatching period of a single generation of eggs in the same environment results in the appearance of susceptible larvae after the earlier-hatching individuals have died of the disease. It may also be noted that if older larvae that survive infection are the source of the disease for the succeeding generation, the number of insect-to-insect cycles is increased from the standpoint of the population if not from the standpoint of a single generation.

Many of the lepidopterous species known to be susceptible to the polyhedroses are univoltine (*e.g. Porthetria dispar* (L.), *Porthetria monacha* (L.), *Malacosoma* spp., *Hemerocompa pseudotsugata* McD. and others). One of the earliest questions in the field concerned the mode of transmission and survival of the virus over the period of several months during which no susceptible stage of the host is present. As indicated in the foregoing, transmission in association with the egg has been recognized and accepted for several years, but is imperfectly understood and has not been described quantitatively in any naturally occurring polyhedrosis epizootic. The present paper includes the results of well-controlled observations which demonstrated this transmission in an epizootic of the disease among a tent caterpillar population.

In addition to transmission with the egg, transmission by persisting contamination of the host plant and environment of the insect has also been suggested. Komarek and Breindl (1924) washed and concentrated by centrifugation samples of soil from a forest infested with a polyhedrosis-diseased population of *Porthetria monacha*. They believed they could recognize polyhedra in these preparations, but their conclusions were not substantiated with infectivity tests. These authors did not believe the pathogenic agent could persist through the winter on the host plant and assumed that contamination in the soil is the source of infection for each generation. Prell (1926) also observed the distribution of the virus over the soil and suggested that this contamination could persist over the several-year period separating outbreaks of the host. More recently Thompson and Steinhaus (1950) experimentally demonstrated the presence of the virus causing polyhedrosis in the alfalfa caterpillar, *Colias philodice eurytheme* Bdvl., in field debris, soil, and irrigation water.

Clark (1955, 1956) reported a series of observations and tests which demonstrated the persistence of the polyhedrosis virus of *Malacosoma fragile* on the host plant between generations of the insect. It was shown that virus applied artificially to the plant survived the winter and was ingested by larvae of the succeeding generation.

The present paper reports a demonstration of the role of this means of transmission of the virus in a natural outbreak of polyhedrosis among a tent caterpillar population.[1]

1956 Tests

Two populations of the Rocky Mountain tent caterpillar were used for experiment and observations during the larval development period of 1956. The populations, described below, are separated by about 190 airline miles.

One population, referred to here as the Arroyo Hondo population, infests quaking aspen, *Populus tremuloides,* in a steep canyon near Taos, New Mexico. In this location, at an elevation of 8,000 to 10,000 ft., the aspen extend along the canyon bottom and up and over the canyon walls. Typically occurring in dense stands, the mature trees are foliated only at the upper 10 to 20 percent of their length. Observations were restricted to younger and marginal trees. The tent caterpillar population has been extremely dense in this area for some time and was serious enough to warrant treatment with an insecticide by the U. S. Forest Service in 1951. Treatment was necessarily restricted to roadside strips and has not affected the over-all population trend. As described in a preceding section, polyhedrosis became evident in 1954 and reached a high rate of incidence and wide distribution by 1956. Mortality was less than 100 percent in 1956 and some population is expected in 1957. A gradient in incidence suggesting a focal point of the disease seemed quite

[1] In the previous papers of this series, tests and observations on tent caterpillar populations in the Sierra Nevada Mountains of California were reported. This insect has been known as the Great Basin tent caterpillar, *Malacosoma fragile* (Stretch) by most authors (Essig 1926; Keen 1952) and was so designated by the writer. Some of the observations reported were made on populations occurring 10 to 20 miles from Virginia City, Nevada, from which Stretch described *M. fragile* (1881). This is the only species of *Malacosoma* known to the writer to occur in the area. The work reported in this paper involved a species of *Malacosoma* in northern New Mexico and Arizona. This species has also been widely regarded as the Great Basin tent caterpillar *Malacosoma fragile* (Stretch). The writer noted in 1955 a distinct difference in color between the caterpillars and the adults occurring in the two areas. The Rocky Mountain form seems to agree with specimens deposited as *M. fragile* in various museums and the California form was regarded as an undescribed species by competent authorities. The writer is informed that original descriptions of species of *Malacosoma* based largely on color are difficult to interpret. In view of the collection in what is in effect the type locality, inadequate descriptions with possible subsequent mis-identification of specimens deposited in museums, and to preserve continuity, the *M. fragile* in this paper refers to the species found in eastern California. The species studied in New Mexico and Arizona is here referred to as the Rocky Mountain tent caterpillar.

apparent along a four-to-five mile stretch of road along the canyon bottom. Data to support this observation were not collected.

The second population, referred to here as the Chuska population, of the Rocky Mountain tent caterpillar used in these tests occurred in the Chuska mountains of the Navajo Indian Reservation. This population also infests quaking aspen as it occurs along the margins of the large open meadows that break the coniferous forest on the Chuska Plateau. This plateau extends north and south at an elevation of 9,000 feet along the northern Arizona-New Mexico boundary.

The Chuska population has been at a high density for a shorter period of time than the Arroyo Hondo population. An extremely dense population was observed on the Chuska Plateau as early as 1955, however. Due to the negative nature of the assertion and the possible occurrence of infection without outward manifestation among older larvae, it probably cannot be stated that any population of a susceptible species is absolutely polyhedrosis-free. If, however, polyhedrosis occurred at all in the Chuska population, it was at such a low incidence that it could not be detected. Over a period of about 40 days a total of 500 tents were examined for larvae with typical virus symptoms. In addition to the 500 tents closely scrutinized, many more were casually examined during the course of the work. No indications of the virus were found. Although an infected larva may die at any place on the plant, because of the fact that the tent caterpillars congregate on the tent at frequent intervals and spend the greater part of the time in this location, the tents are the heaviest sites of concentration of infected larvae. The tents form the most effective units for observations and sampling of disease incidence. No effect of polyhedrosis on the infected larvae, such as the tendency of infected larvae of *Porthetria monacha* to climb to the highest part of the tree, has been observed among tent caterpillars.

The tests reported involved the reciprocal transfer of egg masses between the "disease-free" (Chuska) and the disease-present (Arroyo Hondo) populations and the observations of appropriate undisturbed controls.

Transmission with the egg

To examine the extent of virus transmission with the egg, 35 egg masses were collected from aspen trees in the Arroyo Hondo population and attached to host trees in the Chuska area. The transfer was made on May 6 and 7, prior to hatching in the Arroyo Hondo area. The incidence of polyhedrosis among these larvae, hatching from egg masses deposited in a virus-present area but developing in a virus-free area, relative to the incidence of polyhedrosis among larvae from undisturbed egg masses in the virus-free area, should indicate the extent of transmission with the egg. Control observations were made on 35 tents formed by larvae from undisturbed egg masses within 75 to 100 feet of the trees receiving the transferred egg masses.

At the time of attaching the transferred egg masses, the receiving host tree was examined for native egg masses which were removed to prevent interference with the test. The abundance and effect of larvae migrating from adjacent and overstory trees was not anticipated, however, and some of the value of the test was lost from their interference. The native population was dense enough to defoliate host trees by the third and fourth instar. Following defoliation, they migrated randomly through the test trees and intermingled with the test larvae. While the intermingling reduced the value of the data on the proportion of the egg masses carrying the virus, it was possible to modify methods of observation to salvage useful and reliable information and to demonstrate transmission with the egg as a natural process.

The first examination of these egg masses was made on May 17. On this date, the aspen buds in the locality of the test were swelling and opening and the larvae were just starting to hatch. No evidence of polyhedrosis was found.

On May 27, most of the larvae were in the first instar. Four egg masses could not be accounted for. By this time, fairly heavy mortality had occurred among larvae from several egg masses, but it was not possible to definitely ascribe this mortality to polyhedrosis. The very small larvae that had died or disappeared could not be found for examination. No definite evidence of polyhedrosis was obtained, but subsequent observations suggest that at least some of the mortality was caused by the virus.

By the examination of June 7, the migrating larvae from the defoliated over-story had invaded and defoliated the test trees. Many of the original tents were still identifiable, however. These tents were removed and, with any larvae remaining within them, were held in sterile vials for later laboratory examination of tent debris and larvae for polyhedra. These examinations were carried out on August 8. Polyhedra were found in 10 of the 17 tents collected.

After removal of the tents, a further examination of the trees for larvae with symptoms of polyhedrosis was made. It was recognized that any dead larvae found at this time could not be identi-

fied as hatching from the introduced egg masses. An incidence of polyhedrosis significantly higher among larvae on these trees than among larvae on control trees, however, would indicate that egg contamination was the source of infection whether the infection was recognized in the original test insects or in subsequently infected immigrants. On June 11, each tree was closely examined; all larvae with indications of polyhedrosis were removed and held in sterile vials for laboratory examination. Examination with the light microscope showed that virus-killed larvae were collected from 13 of the 31 test trees.

With each examination of the larvae on the test trees, an examination of 35 tents in the control area was made. No evidence of polyhedrosis was found in the control area throughout the period of the test which extended from hatch to the onset of pupation.

Host plant contamination

As the reciprocal of the Arroyo-Hondo-to-Chuska transfer, 75 egg masses collected in the Chuska infestation were tied to trees in the Arroyo Hondo area. Trees receiving the egg masses were selected from the understory, and were examined for native egg masses which were removed. The collection of egg masses from the Chuska population was made in the area of the control observations made for the Arroyo-Hondo-to-Chuska tests. In this way, these observations served to determine the extent of polyhedrosis in the population of egg masses from which those transferred to Arroyo Hondo were drawn.

The incidence of polyhedrosis among larvae hatching from egg masses collected in a virus-free area but developing in a virus-present area, relative to the incidence of polyhedrosis among larvae developing undisturbed from egg masses in the virus-free area, should indicate the extent of transmission of the virus by host plant contamination.

The egg masses were collected and transferred to Arroyo Hondo on May 5 and 6. Unfortunately the state of spring development was not synchronized in the two areas. Development of the Chuska egg masses had proceeded to the point where the larvae started to emerge at the time of the transfer. Development of the host trees at Arroyo Hondo, however, had not reached the point of bud opening. Many of the early hatching Chuska-to-Arroyo-Hondo larvae were lost through starvation.

It was possible to observe the eggs of this transfer twice through the period of larval development.

On June 2, the results of the delayed appearance of foliage on the host plant were apparent and many larvae had already disappeared. The surviving larvae were mostly second instar. No evidence of polyhedrosis was found. On June 23, larvae could be found on only 9 of the original trees. On all but one of the 9 trees, polyhedrosis-killed larvae were clearly evident. Subsequent examination by light microscope confirmed the presence of the disease. As indicated in the description of the Arroyo Hondo population polyhedrosis-killed larvae were prevalent throughout the area. The control egg masses, as noted above, were free of polyhedrosis.

Discussion

Although the interference of migrating larvae and the lack of synchronization prevent a quantitative evaluation, the tests demonstrate that both means of survival and transmission are effective between generations in a natural epizootic of the disease.

While the recognition of both these factors is essential in drawing a preliminary hypothesis on the ecology of the disease relationship, it will also be necessary to gain an understanding of the relative effectiveness of each. Persisting host-plant contamination can be considered an important factor in transmitting the disease in a given area, but it is obviously not a primary factor in the spread of the disease in space. Transmission of the virus by the adult with the egg seems to be the most likely factor yet recognized in the spread of the polyhedrosis of the tent caterpillar. Steinhaus (1954a, p. 216) quoted the author as having ". . . noticed that in the case of tent caterpillars, the 'momentum' of a virus-caused epizootic may extend a disease in time as well as in space." Unfortunately, the writer has not yet had the opportunity of observing the extension in space of an epizootic among tent caterpillars; nor does he have more than a vague notion of what constitutes the "momentum" of an epizootic. It is, in fact, not clear whether a polyhedrosis epizootic among a tent caterpillar population does spread in space from one or more focal points or whether it appears more or less simultaneously throughout the large areas frequently involved.

Fundamental to this problem is the question of the original source of the disease in a given population. Stated another way, this is the question of the survival and transmission of the virus between outbreaks or occurrences of the susceptible insect species in a given area or its introduction from other sources.

At the present time it appears useful only to extend an hypothesis for future testing. The simplest hypothesis consistent with the available information seems to remain Prell's (1926) belief that the causal agent could remain viable in the

soil for a period of several years. The saturation of an area with polyhedra following an epizootic of polyhedrosis which has destroyed the population is well known to anyone familiar with the phenomenon. None of the accumulated facts concerning the resistance of the virus to environmental factors refutes the assumption that the virus, within the polyhedra, can remain viable in soil and soil debris for a period of several years. Undoubtedly some diminution would accrue through loss of infectivity as well as mechanical removal by precipitation and wind. It is considered, then, that at the termination of the host insect outbreak by polyhedrosis, large quantities of the infectious agent are deposited in the environment and that the pathogen persists, though decreasing in volume, for a period of years. If the host insect reappears during the period of survival, the disease is again manifest; if the reappearance of the host does not occur until after the period of survival, the virus does not appear in the population unless introduced from an outside source.

A second possible means of survival of the virus between outbreaks of the host involves its passage at a very low incidence among the residual host population remaining in the area. The extent of such a residual population and the occurrence of the disease among populations of tent caterpillars which have survived a polyhedrosis outbreak are too poorly known to permit more than recognition of the possibility. The two means of survival, however, are by no means mutually exclusive.

Available information also warrants consideration of the dynamics of the reappearance of the disease in the tent caterpillar populations following, perhaps by several years, an earlier population which was destroyed by polyhedrosis. If the source of the virus is soil contamination, the virus obviously must be moved onto the food source of the larvae. Prell (1926) suggested dissemination by the wind. Komarek and Breindl (1924), who assumed that the causal agent could not survive one winter on the host plant, believed that wind dissemination of the polyhedra in the soil was the distributing agent between generations. Earlier, Glaser and Chapman (1913) could not detect, by feeding tests, wind movement of the virus over a space of a few inches. Thompson and Steinhaus (1950), on the other hand, found that a fan-generated wind of four m.p.h. transported the polyhedra of the alfalfa caterpillar a maximum of two feet when the source was freshly dead larvae clinging to the host plant. Movement of polyhedra from dried larval remnants could not be detected. These authors stated that when the larval remnants were mixed with soil, however, an air current would move the polyhedra at least six feet.

Usually tent caterpillars do not come into contact with the ground until the larvae leave their host plants after defoliation or prior to pupation. These larval movements, as well as the movements of other arthropods, may also distribute the virus through the environment.

With either mechanism of movement of the virus, the increase of incidence of polyhedrosis to the level of destruction of the population would appear to require considerable time. The original inoculum from wind or arthropod disseminated virus is likely to be very small. Our experience indicates that an infection initiated in this manner is not likely to be manifest until late in larval life or perhaps in the next generation through transmission with the egg. If only a small proportion of the caterpillar population is infected directly from virus in the environment, the time required for a high incidence of larval mortality could amount to several years.

In a previous paper (Clark 1956), the writer considered the role of the transmission of the virus by plant contamination in relation to the density of the tent caterpillar. It was stated that the probability of the infection of a larva from this source seems to be a function of the proportion of the plants in the stand infected and contaminated by diseased larvae of the preceding generation, and of the proportion of plants on which egg masses of the succeeding generation are deposited. It was also stated that this suggests that transmission by host plant contamination would appear to become increasingly important with increasing host population densities. It may be equally reasonable to expect a host density threshold below which transmission by host plant contamination does not contribute to the increase in incidence of polyhedrosis. It remains possible that a given density of the host could so thoroughly distribute the virus over the area that great increases of host density above a minimum would not be reflected in increases in the proportion of larvae killed by the disease. As was recognized earlier, transmission by this means is only one factor involved and we have no information on which to base a quantitative evaluation of its role.

Steinhaus (1954) poses the question: Are insect diseases density-dependent?; and argues that all infectious diseases of insects should be so considered. This contention is largely based on descriptions, taken from the literature, of the destruction by disease of very dense host populations. Actually the suggestive value of these gross correlations has been long since extracted. It was, in fact, observation of the frequent coincidence

of high disease incidence with high host-density that in large part led Howard and Fiske (1912) to erect their category of facultative mortality factors. Facultative factors, of course, are now known as density-dependent factors. Steinhaus' argument, which neither challenges the original concept of facultative factors nor adds new information, appears to be a circular effort in that he fits insect diseases into the category which was originally erected to accommodate them.

The sources of error limiting the value of correlations such as those used by Steinhaus should be too well known to require enumeration, and at the present time it would seem most useful to regard the effect of changing host densities on polyhedrosis incidence as one of the important questions in the ecology of the tent caterpillars. It is true that we can recognize certain mechanisms of spread of the disease as being at least partly influenced by host density. In addition to consideration of the virus contaminating the host plant, we can recognize that not only the numbers of migrating larvae but the time of the onset and the duration of such migration may be a reflection of their density insofar as these movements are stimulated by the destruction of their food. Larval movements have not yet been established as a factor in the spread of the disease, however, and we are completely unable to assign quantitative values to any of the factors involved.

Summary

This paper is concerned with the means of transmission of the polyhedrosis of the tent caterpillars, *Malacosoma* spp. A brief review of other aspects of the disease is given to facilitate the discussion of the ecology of the disease.

A characteristic of the polyhedroses of susceptible lepidopterous species is their frequent occurrence at high rates of incidence after the host insect has maintained a high density for several years. It is recognized that we have very meagre or no information on the occurrence of polyhedrosis during the early years of high populations or among unrecorded low populations of the host.

Tests which demonstrated the transmission of the virus by host plant contamination and in association with the egg in a natural epizootic of the disease are reported.

To determine transmission on the host plant, egg masses were transferred from a virus-absent area to a virus-present area; polyhedrosis was found among larvae from these egg masses. The reciprocal transfer was made to determine transmission with the egg; polyhedrosis was found among larvae from egg masses transferred from the virus-present to the virus-absent area. Control observations were maintained on larvae from undisturbed egg masses in the virus-absent area, and no larvae with symptoms of polyhedrosis were detected in the control group.

An hypothesis concerning the transmission of the disease between outbreaks of the host insect is considered for testing. Available information on the resistance of the virus, as it is occluded within the polyhedra, suggest that the causal agent is capable of persisting as a contaminant in the environment for the several-year period involved. If this contaminant is the source of inoculum for a succeeding population it must be moved onto the leaves of the host plant and ingested by the larvae. Wind and movements of the host larvae and other arthropods are possible agents in this distribution. Survival, transmission, and distribution by these factors would probably require considerable time before the disease reached a high level in the population.

Although we can recognize certain mechanisms in this transmission which are possibly influenced by the density of the host, we are justified only in regarding the effects of the host density as an important question in the problem.

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ON THE MOVEMENTS OF CERTAIN BERMUDA REEF FISHES[1]

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Our knowledge of habits of reef fishes is limited; there are several taxonomic studies of reef fishes in the Atlantic but only two of them deal to some extent also with fish habits. (Longley and Hildebrand 1941; Beebe and Tee-Van 1933.)

This study aimed at the investigation of movements among several reef fishes, the permanence of their residence in certain areas, and their tendency to return to a "home" reef after transfer to another.

Long- and short-term movements are customarily investigated by marking or tagging. Larger numbers can usually be marked among schooling than solitary fish. Few of the larger reef fishes travel in sizeable schools, some form small groups, others pair and many of the large carnivores are solitary. Relatively small numbers of fish were tagged in this study, mostly because of their habits and the difficulty involved in such operations from a small boat in the open sea. The high percentage of returns in several species, however, should make up for this shortcoming.

The study was carried out between July 1955 and September 1956 with periods of intensive trapping and marking in one area during the summer of 1955, in February and March 1956 and again during the summer of 1956. Localized trapping was supplemented by recaptures of tagged fish in other areas, giving information about the rate of emigration from a reef and about distances traveled. Diving observations were also drawn upon.

MATERIALS AND METHODS

Location of Study Area

The Bermuda Islands at 32 N. Lat. and 64 W. Long. are the northern limit of coral reef biota in the Western Atlantic. Reefs extend over 170 square miles (Fig. 1) and surround the Islands at variable distances, forming a narrow belt of breakers close to the Islands in the south and larger expanses toward the west, north, and east. New coral growth accumulated since the end of the Pleistocene forms only a thin veneer over the substratum of aeolian limestone (Verrill 1907).

Traversing the northern reefs towards their outer edges many isolated reefs of one to several acres are encountered mainly on the landward side. Farther out toward Bermuda's steep slopes, reef areas become larger and unbroken.

A group of such small reefs was selected as the study area because of their convenient location with respect to our base, the Bermuda Biological Station for Research, and because they appeared

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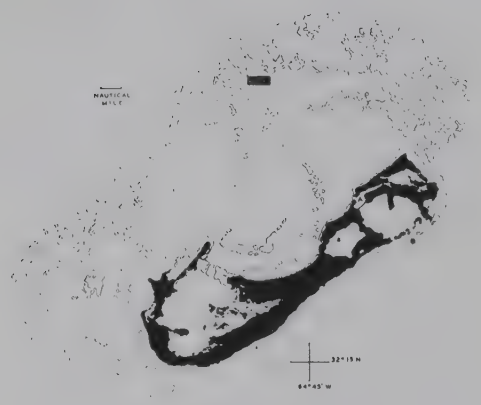

FIG. 1. Bermuda and Reefs, showing location of study areas.

representative of the Bermuda reef environment. Figure 1 illustrates their overall location and Figure 2 their distance from, and relative position to, each other. My assistants named the individual reefs and we found that it indeed greatly facilitated our work to be able to refer to certain locations by name.

FIG. 2. Map of study area: T_1, Twin Reef #1; T_2, Twin Reef #2; B. F., Bardach's Folly; C. R., Carl's Reef. The dotted regions represent sandholes.

These reefs rise from a sandy bottom at 40 to 55 feet to their highest crests, 3 to 5 feet below the surface. Figure 3 is a map and an elevation sketch of "Bardach's Folly," a reef of 2.47 acres (1 hectare) on which more than half of the trapping and tagging was done. Like other similar reefs, is it dotted with large and small sandholes; in some cases these make up as much as 1/3 or more of the total reef surface.

The following fishes were tagged or marked

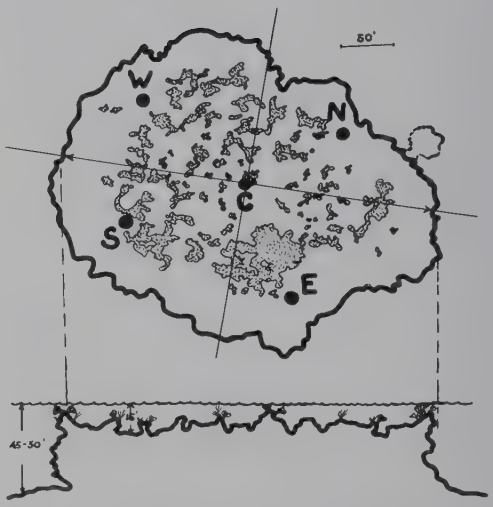

FIG. 3. Map and elevation sketch of Bardach's Folly indicating location of traps for movement study. The dotted areas are sandholes; sea fans are also indicated on the cross section.

and some individuals were recaptured five or six times in the course of a year:
Holacanthus bermudensis (green angelfish), *Acanthurus* spp. (surgeonfish), *Scarus vetula* (*S. gnathodus*), *Sparisoma viride* (parrotfish), *Epinephelus guttatus* (red hind), *E. striatus* (Nassau grouper), *Mycteroperca* spp. (groupers), *Cephalopholis fulvus* (coney), *Haemulon sciurus* (blue-striped grount), *Lutianus griseus* (gray snapper), *Holocentrus* sp. (squirrelfish).

Trapping and Tagging Proccdure

Baited Bermuda fish traps were used for securing the fish. These are made of galvanized chicken wire, reinforced with the wood of a local shrub (spicewood) which is heavy and withstands immersion in salt water. The traps are either pentagonal or oval and have one, seldom two, inset funnels with a downward opening. They were 3 to 4 feet long and 2 or 2½ feet high. They are baited and thrown into the desired location from the boat and raised with a grapple hook. On Bardach's Folly they were placed on, or close to, pre-set metal markers on the bottom (Fig. 3) and on the other reefs they were always placed near the same sandholes so that their position varied little from set to set.

Small bait fishes such as *Sardinella anchovia* or hemiramphids were used most frequently; if these were not available, miscellaneous other small fish we secured by seining.

In 1955 numbered red plastic tags were affixed to the fishes' body, anterior or posterior to the dorsal fin (Joëris 1952). In February 1956 we changed to Monel metal clip-on tags which were placed either around the maxiliary bone, or on the operculum.

Parrotfish proved delicate when handled and were fin-clipped as the quickest and least damaging method of marking. Since length measurements were also taken most individual fish could be recognized over short periods of time. The fish were released close to the location of capture or were transferred to another reef.

Observations and Discussion

Homing Experiments

Many reef fishes habitually hide under ledges or in holes. Some defend a territory and often fishermen or skindivers assert that the same fish may be encountered upon return to the same location, even after years. This suggests definite home ranges and poses the questions whether and how the fish might recognize specific reef areas.

Between June 20 and August 30, 1956, four fish traps were set on each one of the two "Twin Reefs" and visited as frequently as weather conditions permitted, at least once a week but usually every 2nd or 3rd day. The fish captured on Twin Reef 1 were tagged and transferred to Twin Reef 2 and vice versa. Of the 176 fish of various species tagged in this experiment only the red hind, the Nassau grouper, and the green angelfish were recaptured in sufficient numbers to give an indication of homing tendency or the lack thereof (Table I).

Table I. Homing Experiment on Twin Reefs near Bermuda, June 20–August 30, 1956

Number	Angelfish	Surgeonfish	Nassau Grouper	Red Hind	Groupers	Squirrelfish
Fish tagged on both reefs...	63	26	14	47	6	8
Tagged on reef 1.....	32	12	8	33	2	5
Tagged on reef 2.....	31	14	6	14	4	3
Recaptures....	27	4	11	12	1	2
Times fish showed homing.....	2	1	10	9	0	1
Times fish showed no homing.....	25	3	1	3	1	1

Angelfish 413 did not return to its home reef after three consecutive trappings within 24 days while 488 was still on the strange reef at the second recapture which took place 35 days after tagging but had returned "home" at the third recapture, two days later.

Nassau groupers and probably also the red hinds have strong homing tendencies but the angelfish do not. Individual fish differ in homing behavior; for instance grouper 1439 returned to its home reef even after the fourth displacement while another individual did not return to the home reef at all. Red hind 566 homed three times within 9, 4, and 29 days respectively but was recaptured on the strange reef after an additional 11 days and the third transfer.

It may be argued that the proximity of T_1 to T_2 would almost inevitably lead to the return of a high percentage of transplanted fish if they "chose" to leave their new home at all. It could also be assumed, however, that they would leave in a random manner unless they have the capacity to navigate and select the direction of departure. About 1/12 (8%) of the perimeter around T_1 and T_2 respectively are taken up by the adjacent reef. Even if some fish swam directly to another reef in the chain and then returned, not more than 10 to 15 percent of the expected total recaptures should occur on the original reef. Total expected recaptures do not exceed half of the tagged fish (Table III, Column 2). With this assumption about 7 percent (one half of 15%) or 3 hinds and one grouper might have been expected to return by chance. Nine hind and 10 grouper recaptures were registered, suggesting, together with the evidence from repeated recaptures, that these two species are prone to return to a definite home range.

Traps were again set on the Twin Reefs for one week in November or 140 days after the beginning of the homing experiment. Six tagged hinds and groupers were caught on Twin Reef 1 and 4 on Twin Reef 2. Two of these 6 had moved to T_1 from Bardach's Folly since the end of August 1956, the remaining 4 were old residents which had returned to their home after one or several transplants. On T_2 the situation was similar with one migrant from B. F. and 3 old residents which had already returned to their home reef during the homing experiment. These further observations are in line with those set forth in the discussion.

When it had become apparent, after about 50 days, that red hinds and Nassau groupers returned to their home reefs, seven individuals of each species were blinded by cutting the optic nerve under chloretone anesthesia before releasing them on the strange reef. None was recaptured and it is most likely that they soon became victims of larger predators or died. Seven other fish of each of the same two species had their interior and posterior nares firmly plugged with cotton. Red hind 510

which was so treated homed between August 20 and 29, presumably without the use of its sense of smell.

Between one and eight fish, each, of several other species, were also tagged and transferred but, apparently the numbers involved were too small to yield any information on their homing tendencies.

Fish Movements on One Reef

Bardach's Folly was used for these observations because in a growth study of certain species done there (Bardach and Menzel 1957), more fish were tagged than on any other reef. The reef surface was divided into the four quadrants of the compass; the center and each quadrant were marked by a lettered metal disc and the traps were set close to them (Fig. 3). Here again only certain species were recaptured in sufficient numbers to give definite results (Table II).

TABLE II. Fish movements on a 2.47-acre reef near Bermuda, summers of 1955 and 1956. Numbers in brackets indicate days between tagging and recapture or between repeated recaptures

Species	No. tagged	No. of times recaptured	No. times moved from one to any other quadrant	No. times did not move out of quadrant	χ^2 based on 25% chance of recapture in tagging quadrant
Angelfish.....	26	33	8 (15+)	25 (9+)	45.20**
Red hind.....	24	46	33 (14+)	13 (5+)	0.25 ns.
Nassau grouper....	12	27	18 (7+)	9 (7+)	0.99 ns.
Gray snapper.	33	5	5 (17)	0 —	.....
Squirrelfish...	6	4	0 —	4 — (2 after 30 days) (2 after 300 days)	.....

There are confounding influences in these observations, such as the presence of bait in the traps, the posible selection of traps as places of refuge (Rodeheffer 1945), the inevitable small shifts in the position of the traps from set to set, and loss of tags. Twenty-seven percent of the tagged groupers lost plastic tags during the first two months; thereafter there was little evidence of further loss. This may be due to wound healing after tag loss and population replacement. The percentage of loss seems high but because most reef fishes often hid in holes in the coral there is no reason to believe that fewer tags were lost by other species.

In spite of these reservations it appears that the angelfish had a strong tendency to stay in small areas not exceeding about half an acre. Red hinds and to some extent Nassau groupers were prone to move more freely over the reef. Chi-square tests strongly supported these findings. The tests were based on the assumption that all species move freely on the reef and that a quarter of all recaptures might therefore occur where they were originally tagged (Table II). When trapped after two weeks, hinds had frequently moved from their tagging locations but when taken within a few days they were usually still in the original location. The tagged groupers were recaptured 27 times with 18 recaptures outside the tagging quadrant; the average interval between tagging and recapture was about 7 days. This might suggest that groupers move somewhat more freely than hinds (see also Table I).

It is interesting to note the the species which were moving freely on the reef and presumably had its entire extent as a range also showed homing behavior. On the other hand the angelfish stayed in a small area without much detectable day-to-day movement and did not return to a home reef. Their chance of relocating such a small home range, if displaced, was negligible.

Too few gray snappers were captured to furnish more than an indication that they also move freely over the reef at least in daytime. When one follows a gray snapper by diving immediately after tagging, the fish joins, or rejoins, a school of his species mates. We could frequently see tagged gray snappers near the bottom of the reef and some were still observed 200 days after tagging. One gains the impression that the entire group is continuously on the move though they remain on or near the same reef. Gray snappers were not seen to feed on their daytime travels; Longley and Hildebrand (1941) mention that the schools break up at night when the fish feed.

Squirrelfish are known to be crepuscular or nocturnal animals. They stay hidden during the day and become active late in the evening and at night. This was borne out by the results of six 2-hour trapping periods during night and day respectively. Three Nassau groupers, 4 red hinds, 1 grouper, 4 parrotfish, and 2 angelfish were taken in the average daytime set while the same traps in the same location during the night yielded an average of 1 red hind, 1 spotted moray, and 5 squirrelfish. All the squirrelfish recaptured in the movement study (Table II) were taken from daytime lifts and we know only that they stray little from their hiding places then or that they return after nocturnal foraging, which may or may not take them far afield (see also Longley and Hildebrand, 1941).

Additional Observations on Habits and Movements

In the total reef fish fauna there are about thirty times the number of species treated here but by weight the various fish discussed below make up

TABLE III. Recaptures of tagged fish on a 2.47-acre reef near Bermuda, 1955/1956

Species	Recaptures, Days After Tagging				Greatest distance travelled	Ratio of Tagged to Untagged Fish on Home Reef	
	No. tagged	30 days Home reef	60 days Home reef	150-300 days Home reef	150-300 days Strange reef		60 days after tagging	180 days after tagging
Red hind	64	32	9	5	4	12 mi	2:1	1:8
Nassau grouper	26	12	5	5	1	1.5 mi	1.7:1	1:2
Other groupers 2 spp.	17	2	0	3	2	1.2 mi	.....	...
Angelfish	65	13	11	15	0	.....	1.1:1	1:8
Surgeonfish	8	0	2	0	0	.....	.....	...

over 80% of the summer standing crop (Bardach and Menzel MS[2]). Some schooling fish such as carangids may, at times, be found on isolated reefs briefly, rarely exceeding half an hour. Large predators such as barracudas and sharks also visit these reefs but usually they roam farther afield, covering large distances in shorter time than even the more mobile fraction of the reef fishes proper.

We have seen that some reef fishes move less than others. The bulk of these observations extended over 2 to 3 months. Some recaptures after 6 months or even a year gave information on long term movements (Table III). In the following discussion on habits and movements of some fishes of a shallow Bermuda reef, tagging and recapture data were supplemented by observations while diving in the same area and details from other concurrent studies.

CHAETODONTIDAE:

Angelfish (*Holacanthus bermudensis*). Recapture figures after 300 days suggest little movement of adults away from the reef; this was the only species where recaptures on the home reef occurred with higher frequency after 300 days. The relatively low ratio of tagged to untagged fish after 60 days may be explained by high tag loss and by inefficiency of baited traps in taking this species.

Young angelfish 1 to 2 inches long can be seen on the reefs after the spawning period of this species in May. Eggs of the black angelfish or rock beauty (*Holacanthus tricolor*) were collected. They were relatively large, just over 1 mm in diameter and had neither oil inclusions nor hair-like or other obvious holdfast mechanism. They sank to the bottom on being released by the female fish (personal communication, Mr. Bronson Hartley).

Butterfly fish (*Chaetodon* spp.). These fish, like the angelfish, usually occurred in pairs. When divers followed them, the two fish stayed close together and at times one appeared to wait for the other. When these fish were observed during repeated half-hour dives they never strayed beyond an area of about 400 square meters. Several pairs of *C. striatus* and *C. capistratus* were captured and the members of the pair were identified as male and female.

Tagging of angelfish and diving observations suggest that chaetodontids spend their entire lives associated with a relatively small portion of the reef environment. Nothing seems to be known about their spawning habits, but because of the nature of the eggs it appears unlikely that they have pelagic stages.

ACANTHURIDAE:

Surgeonfish (*Acanthurus chirurgus, A bahianus*). These are the two common Bermuda representatives of the family; they occur in the same environment and seem to be similar in feeding and schooling habits. No distinction of the two species was made in tagging. Though a few were tagged on Bardach's Folly, none was recaptured on adjacent reefs.

Surgeonfish are usually not taken below 10 fathoms and a large portion of the small herbivorous fish on the reef is made up of young surgeonfish of the year. Several 30-minute diving observations at various hours of the day when browsing schools of surgeonfish were followed did not lead the diver beyond the confines of 500 square meters.

These observations suggest that here again we deal with permanent residents of relatively small areas of the shallow reef environment.

POMACENTRIDAE:

The species of this family are usually small in size and are known for their strong territorial tendency (Longley and Hildebrand 1941; Beebe and Tee-Van 1933). They make up a sizeable portion of the complement of small fish on the reef

[2] Bardach, John E., On the summer standing fish crop of a shallow Bermuda reef. (MS in preparation.)

inasmuch as one encounters at least one pomacentrid every five meters or less when one follows a transect over active coral growth.

Five sergeant majors (*Abudefduf saxatilis*) were tagged on Bardach's Folly and two were recaptured there within 30 days and one was seen by a diver after 50. They appeared to range over the entire reef.

Several marked territories of *Pomacentrus fuscus* and *P. leucostictus*—(perhaps color phases of the same species)—were revisited throughout forty days during the summer and the fish were found in the same locations. These facts and our knowledge of their egg laying and guarding habits suggest that *Pomacentrus* live out their entire life spans in a small area of reef environment.

SCARIDAE:

Parrotfish are a prominent and conspicuous part of the reef fauna. They proved to be delicate and excitable when captured. Sixteen of the 22 parrotfish of mixed species which we tagged in 1955 were observed to sink to the bottom and lie on their sides; several of them were recovered dead 30 minutes later. They seem to withstand fin clipping, however, if it is done carefully and under water. A few parrotfish were thus marked in 1956, and some information on their movements was obtained.

Five *Sparisoma viride* were marked on Twin Reef 1 and two of these were recaptured there after 32 days. Direct observations revealed them to chase each other but whether this behavior was associated with feeding or breeding habits could not be ascertained.

Three individuals of *Scarus vetula* were finclipped and one of them was recaptured on Carl's Reef, another reef adjacent to those already mentioned. I also followed a school of 1 male and 5 female *S. vetula* (formerly *S. gnathodus*, but now established as the female or immature color phase of *S. vetula*—Winn and Bardach 1957) for over 30 minutes on their feeding movements and found myself over 150 m from my starting position when the declining air supply of my aqualung forced me to return to the boat. The fish were then still moving in the original direction. If this distance covered is typical it may suggest that this species of parrotfish, at least, often moves over larger areas than our study reefs.

SERRANIDAE:

Very few serranids under 4 inches long are seen on the outer reefs and even those that were observed seemed scarce compared to the adults. The larvae of some representatives of this family are suspected of being pelagic because (a) their closest Mediterranean relatives have pelagic larvae (Lo Bianco 1933), and (b) a fish larva from a surface plankton tow taken 5 miles to the southwest of Bermuda over 1000 fathoms of water developed into a Nassau grouper in one of the tanks of the Bermuda Biological Station for Research.

Some serranids reach a very large size; besides the well known jewfish (*Garrupa nigrita* and *Promicrops itaiara*) of several hundred pounds from deeper water, members of the genus *Mycteroperca* also grow to a hundred pounds or more, and Nassau groupers over 40 pounds have been taken in Bermuda waters.

Most of the larger individuals of these species occur in deeper water but those species of the family which reach a maximum of only several pounds may be taken at all depths. This was borne out by a comparison of trap catches at different depths. The average weight of serranid fishes per trap from 73 traps set between 2 and 9 fathoms was 1.57 kg (3.45 lb) while each of 102 traps set between 10 and 30 fathoms caught 3.24 kg (7.2 lb). The average weight of the fish taken in the deep traps was about double that taken in the shallow and there were also more of them. Rockfish and Nassau groupers were more heavily represented in the deep catches while red hinds and coneys (*Cephalophovis fulvus*) predominated in the shallows.

No sexually mature individuals of the larger groupers were taken on our study reefs and they are generally rarely taken in shallow water while the smaller species seem to grow to maturity at all depths.

Most of tagged seranids stayed on the reef for about a month (Table III). After two months considerable exchange of fish between reefs seems to have taken place and after a year a virtually new group appears to be present. Some mortality has undoubtedly contributed to the low ratio of tagged to untagged fish after 180 days but we have no information on the extent of this factor. Spawning concentrations of hinds and groupers have been reported by local fishermen to occur in the spring but it could, again, not be determined whether the exchange of fish is due to increased movement at spawning time or to other causes.

Juveniles of some larger groupers occur in the shallow reef environment but we do not know whether the young of these species also occur in deeper water where most of the adults are found. They probably are distributed with equal frequency of the lower limit of their depth because, on becoming demersal, pelagic larvae would most probably settle where they happen to sink.

The predominance of juvenile over adult of *E.*

striatus and the several species of *Mycteroperca* in the shallow reef poses the question whether or not these individuals move into deeper water as they mature. All that became apparent from our tagging experiments was that some sexually immature groupers stayed on one shallow reef for a year or longer. Whether or not these individuals lived in the "best" hiding places could not be ascertained. Other fish of the same species moved about a good deal more.

There is no evidence that the red hind migrates to greater depth as the fish mature; tagging data and depth/weight distribution suggest that they remain at a given level of the reef environment. Long-term tagging results show that some of them move for short, others for considerable, distances. Several hinds tagged on Bardach's Folly were recaptured on each of the adjacent reefs and one of them was taken 12 miles from its tagging location after over a year.

The coney (*Cephalopholis fulvus*) has habits somewhat comparable to those of the hind. It was less common on the study reef than on the more extended areas of active coral growth farther out towards the breakers. Only 11 fish of this species were tagged and 2 of them were recaptured near their tagging location within 60 days. Diving showed them to be the most secretive of the serranids; they only leave one hole to dart into another. Even when attracted to a baited hook they dash out after it from a hiding place rather than stay around it for any length of time as some of the other serranids and other fish are wont to do.

Coneys occur in graduated color phases from the shallows, where they are brownish-black, down to 40 fathoms or more, where they are bright red. Intermediate colors prevail at intermediate depths. These colors are due to different amounts of melanins and carotenoids in the skin of specimens from any one depth (Bardach MS[3]). The fish cannot change their color rapidly, but only their pattern, and if one of the deeper specimens can be kept alive, it will take several months before the color change becomes apparent (private communication Mr. L. S. Mowbray, Director, Government Aquarium, Bermuda). The coney thus probably remains at one depth for its adult life and there it may move along restricted contour intervals.

HAEMULIDAE:

Isolated reefs have large schools of blue-striped grunts (*Haemulon sciurus*) associated with them; we counted over 350 of them in 1955 and again in 1956. They stay near the bottom of the reef where it rises from the surrounding sand. They presumably feed there and on the reef during the night but have their hiding places under coral and rocky overhangs, winding in and out of them while circling the reef. We only tagged eight grunts because few traps were set near the bottom. Tagged fish, with their bright red plastic discs, stood out clearly, even in a large school. They were still observed with the same group of over 300 fish as long as 200 days after tagging. Similar schools of grunts were found in all comparable reefs and it seems likely that these crustacean and mollusk feeders (Longley and Hildebrand 1941) remain in the same area for the duration of their adult lives.

On a reef, fish are easier to observe than in almost any other type of aquatic environment. The animals are tame and the water is warm and clear. Plentiful and widely distributed as reef fishes are, their distribution is at variance with that of biologists and this explains the many gaps in our knowledge of their life histories and habits.

Summary

Reef fishes of several species occurring in Bermuda waters were tagged and recaptured repeatedly. Underwater observations of their behavior were also made. The tagging and study area was located among several isolated reefs to the north of Bermuda. It was found that only some individuals of several species of serranids remain in the same area for over a year. Many red hinds (*Epinephelus guttatus*) and Nassau groupers (*E. striatus*) move freely from reef to reef during a twelve month period. However, when fish of these same species were transplanted from one reef to another, several hundred feet away, and observed over a period of two months, most individuals were found to return to the reef on which they were originally tagged.

The smaller and partly herbivorous green angelfish (*Holacanthus bermudensis*), surgeon fish (*Acanthurus* spp.) and several species of pomacentrids were found to be more restricted in their movements than the larger carnivores and it is probable that they spend their entire life cycles in a small reef area. Failure to return to an original tagging location when transplanted appeared to go hand in hand with the small ranges of these species.

Additional observations on habits and movements of several other reef species are also given.

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A NOTE ON STATIONARY AGE DISTRIBUTIONS IN SINGLE-SPECIES POPULATIONS AND STATIONARY SPECIES POPULATIONS IN A COMMUNITY

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In this note a logical ecological proposition is derived. There are two implications to this procedure. First, since the consequence is logical, its truth should not require independent experimental evidence (for ecology has hitherto been logical). For the same reason, the statement derived contains no really new facts. It is, however, not at all obvious and consequently seems worth presenting.

The changes of a very general animal population can be described by the following equations, where $x_1(t), x_2(t) \ldots x_n(t)$ are the numbers of individuals in age classes $1, 2, \ldots n$ (respectively) at time t.

$$\begin{aligned} x_1(t+1) &= b_1x_1(t) + b_2x_2(t) + \ldots + b_nx_n(t) \\ x_2(t+1) &= s_1x_1(t) \qquad (1) \\ &\cdot \\ &\cdot \\ &\cdot \\ x_n(t+1) &= s_{n-1}x_{n-1}(t) \end{aligned}$$

Here the b's and s's are birth and survival rates varying with the age distribution. Notice that, for $i > 1$, x_i cannot increase or maintain a constant positive population when x_{i-1} is zero. The population age distribution at time t can be represented by a point in n-dimensional space whose components are $x_1(t), \ldots x_n(t)$. Equation (1) shows what point will then represent the population at time $t+1$. In other words, equation (1) describes the motion of a point through n-dimensional space. This space will be called population space for the rest of this paper.

Some definitions will simplify the discussion. A population of a species will be called type S if small changes in the age distribution result in small changes in the birth and survival rates of the various age classes (*i.e.*, the latter are continuous functions of the former) and if there are two total populations $P_0 > 0$ and $P_1 > P_0$ such that a population between these numbers in magnitude remains between them. This means that the population must grow when it is very small and decrease when it is very large, irrespective of age distribution.

An age distribution will be called "stationary" if the number of individuals in each age class remains constant from generation to generation. This stationary distribution is also stable if any small population change will be followed by a return toward the stationary distribution. Stability will not be discussed in this note as its treatment requires other methods.

The main result of this note is now easy to state. If a species' population is of type S, then there exists a stationary age distribution. This theorem is a direct consequence of the Brouwer fixed point theorem of combinatorial topology (Pontryagin 1952). This theorem states that, for any integer n, a continuous function mapping an n-simplex into itself leaves at least one point fixed. An n-simplex is the nth term in the sequence: triangle (a 2-simplex) and tetrahedron (a 3-simplex); that is, an n-simplex is formed from an $n-1$ simplex in the same manner that a tetrahedron is formed from a triangle.

Now, if there are n age categories, population space is n-dimensional. Furthermore, the region in population space in which the population must ultimately remain (*i.e.*, the region defined by $x_i(t) > 0$ for $i = 1, \ldots n$ and $P_0 \leqq \sum_{i=1}^{n} x_i \leqq P_1$)

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is topologically equivalent to an n-simplex; (mathematically they are homeomorphic). Thus the fixed point theorem applies to this region; hence there must be a point within this region which is a stationary age distribution.

Completely analogously, if the x's represent the populations of n species in a community of type S, then there is a stationary species composition i.e. each species has its stationary population.

The foregoing theorems do not imply that all populations which fail to be of type S must necessarily fail to have a stationary state. That there are unstable populations, which of course must not be of type S, is shown by the following special case of equations (1).

$$x_1(t+1) = b_2 x_2(t)$$
$$x_2(t+1) = 1/2\, x_1(t)$$

where b_2 can be arbitrary except that it vanishes when $x_1 \geqq 1/2\, x_2$. This population can clearly oscillate perpetually. This fails to be of type S since when $x_1 = x_2$ the population always decreases and there is no $P_0 > 0$ as required.

The author is indebted to G. E. Hutchinson for valuable suggestions and criticisms.

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NEAREST-NEIGHBOUR DISTANCE MEASUREMENTS FOR THE ESTIMATION OF ANIMAL POPULATIONS

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Although the problem of assessing populations by measuring the distance from a randomly chosen organism to its nearest neighbour does not, in theory, depend on the nature of the organism, the use that can be made of the theory does depend on whether or not the organism is mobile. This distinction of mobility is substantially that between animal and plant populations. For most animals, population estimates from such data will have to be compared with those based on capture-recapture or other techniques rather than with direct counts. Moreover, there is a special need to compare complementary methods of estimation when no direct count is, in general, available to throw into relief discrepancies between theory and practice.

The Relation between Density and Nearest-Neighbour Distances

Two different expressions have been proposed to link the distances between nearest neighbours and the density of the population. Craig (1953) develops the relationship

$$m = \frac{-k}{a^2 \Sigma log_e \left\{1 - \frac{\pi r_i^2}{4a^2}\right\}}$$

where m is the density, k the number of distances measured, a^2 the area being sampled, and r_i is the distance between the i th randomly chosen insect and its nearest neighbour.

Craig's formula can be simplified, if, as will usually be the case in experiments with animals, the distance between nearest neighbours is of a smaller order than the square root of the area being sampled, in effect if $r_i^2/a^2 < 0.01$. Then the approximation $-x = \log_e (1 - x)$ is sufficiently accurate and the formula reduces to

$$m = \frac{4k}{\pi \Sigma r_i^2}$$

This expression of Craig's was expressly intended for the estimation of population density, but it is distinct in much more than intention from that used by Clark and Evans (1954) among others, and meant by them to estimate degrees of non-randomness in populations whose density was already known. This expression is

$$m = \frac{1}{4\bar{r}^2}$$

where $\bar{r}$ is the mean distance between nearest neighbours. These differences persist even if we ignore the asymmetry of the distribution of r and put $\bar{r}^2 = \Sigma r_i^2/k$. The properties of the distribution of nearest-neighbour distances have been discussed by Skellam (1952) and by Thompson (1956).

Three distinct ways may be noted in which these methods of linking density and distance between nearest neighbours can differ according to the choice of mathematical model. What is probably the least important of these ways arises from the asymmetry of the distribution of r, the positive skewness of this distribution ensuring that $\Sigma r_i^2/k$

is greater than $\bar{r}^2$. A more serious discrepancy arises from the fact that, even for a theoretical population distributed entirely at random, which condition is necessary for the valid application of either expression, the population estimates obtained from Craig's mathematical model will always be higher than those obtained from the Clark-Evans model by a factor of $16/\pi$. It is important to note that this disparity is inherent in the algebraic expressions for each model, and has nothing whatever to do with the purposes for which either model was intended, nor with the third source of difference, the possibly unequal sensitivity of the two models to non-randomness in the population to which they are applied. The factor $16/\pi$ is obtained simply by comparing the simplified form of Craig's expression (putting $\bar{r}^2 = \Sigma r_i^2/k$) with the Clark-Evans expression, algebraically.

The third source of discrepancy between the models, namely differential sensitivity to non-random dispersal, is a difficult problem to investigate theoretically, because there are various kinds as well as various degrees of non-randomness. At least in the first instance, an experimental exploration of the problem seemed easier, as reported later in this note.

Some experimental test of these two ways of linking density and distance is evidently needed, since it is not at all clear that one of them is better founded theoretically than the other; indeed the critical point at which Craig's approach can be said to diverge from that of Clark and Evans is obscured by the greater sophistication of Craig's mathematical technique. Nevertheless, one cannot ignore the fact that the two methods will nearly always differ by a factor of about 4 in their final estimates, since such a discrepancy is large compared with the order of experimental error even in ecological investigations.

Generally, in phytosociological studies, the Clark-Evans approach has yielded reasonable population densities when compared with known values (Cottam and Curtis 1956). However, this superiority need not always apply, and an experiment with animals seemed likely to yield a broader generalisation.

Experiments with Grasshopper Populations

Two field experiments were performed to test the merits of the two mathematical models in practice. During the first trial 334 adult grasshoppers of the species *Chorthippus parallelus* (Zett.), *C. brunneus* (Thunb.), *Omocestus viridulus* (L.) and *Stenobothrus lineatus* (Panz.) were marked with aluminium paint on the pronotum. The insects were effectively confined within an area of 6,400 sq. ft. of ungrazed meadowland at this Field Station near London (this isolated area is designated "colony 3" by Richards and Waloff 1954). The next day a predetermined number of 50 marked insects were recaptured in a total sample of 300 grasshoppers. The estimate of the total population within this area (Table I) has then a known variance (Bailey 1951).

Table I. Population estimates made by different techniques

Experiment	Technique	$\Sigma r_i^2/k$	$\bar{r}^2$	Total pop.	Approximate 95% fiducial limits
English	Marking (capture-recapture)	....	....	2009	1423 2585
	Nearest neighbour (Craig's formula)	520	....	2257	1689 2825
	Nearest neighbour* (Clark-Evans' form.)	....	440	523 (931)	....
French	Marking (capture-recapture)	....	....	562	382 742
	Nearest neighbour (Craig's formula)	4926	....	832	598 1066
	Nearest neighbour* (Clark-Evans' form.)	....	3378	238 (424)	
French; less copulating pairs.	Nearest neighbour (Craig's formula)	5597	....	733	512 952
	Nearest neighbour* (Clark-Evans' form.)	....	4362	184 (318)	
First random artificial population	Known value	....	....	500	
	Nearest neighbour (Craig's formula)	113	....	1160	
	Nearest neighbour* (Clark-Evans' form.)	....	87	369 (653)	
Second random artificial population	Known value	....	....	500	
	Nearest neighbour (Craig's formula)	19.1	....	1331	
	Nearest neighbour* (Clark-Evans' form.)	....	15.5	323 (568)	
Artificial population with restricted randomisation	Known value	....	....	336	
	Nearest neighbour (Craig's formula)	57.3	....	831	
	Nearest neighbour* (Clark-Evans' form.)	....	51.1	183 (325)	

*Estimates with Cottam-Curtis adjustments given in parentheses.

On the same occasion the distances between 50 haphazardly chosen individuals and their nearest neighbours were measured by first marking the position of one insect with a painted stick, and then shuffling round this position in a tight spiral until another grasshopper was flushed. The movements of the first insect must, naturally, be ignored. The population within this area was calculated from the capture-recapture data (Bailey 1951) and according to the expressions of Clark and Evans and of Craig. Approximate 95% fiducial limits are attached to these estimates in Table I, except for the Clark-Evans values, which are given with and without the adjustment

proposed by Cottam and Curtis (1956) to compensate for the fact that the process of sampling from the insect nearest to points chosen at random underestimates the population in that pairs of insects lying further apart than the mean distance are relatively too frequently sampled.

The second experiment was carried out on a population of grasshoppers in Southern France, in a limited plateau of 322 m^2 of scrub on the Mediterranean foothills of the Maures mountains, in conjunction with Dr. F. O. Albrecht, to whom I am grateful for the facilities which made this experiment practicable. Seventy-nine adults of many different species were marked as before, and the next day 35 of these were recaptured in a total of 255 individuals. Table I shows that when a sample of 50 "nearest-neighbour" distances were taken immediately after the recaptures were made, the estimated populations were, as in the English experiments, in substantial agreement with the capture-recapture estimates when Craig's formula is used and seriously low when the Clark-Evans formula was used.

Two obvious explanations for the inadequacy of the Clark-Evans formula, even when adjusted, are the non-randomness of the distribution of the grasshoppers, and a bias in the capture-recapture estimates. This last point has already been investigated by Richards and Waloff (1954) who compared population estimates obtained by capture-recapture methods with those obtained by direct sweeping, and found good agreement. Their experiments were conducted on a population of grasshoppers in meadowland similar to, and within a short distance of, that in which the present English experiments were performed. That three such different methods should exhibit the same bias is improbable.

The Effects of Non-Randomness

The French experiment throws some light on the effects of grouping, because six of the 50 distances there sampled were virtually zero, as between copulating pairs. If this grouping is eliminated by deleting these six records from the 50 originally made, the Clark-Evans estimates are even lower than before, so that grouping, of itself, is unlikely to be the reason for the low values of the Clark-Evans estimate relative to the capture-recapture estimate. Such grouping constitutes over-dispersion; the effects of under-dispersion remain to be investigated.

Since under-dispersion is difficult to simulate in the field, three artificial populations have been constructed of points on graph paper. Two of these empirical trials consisted of truly random collections of 500 points each, the coordinates of the points being drawn from random number tables, as were those of sub-sets of 350 and of 200 points the distances to whose nearest neighbours were also measured. These two tests provide empirical evidence of the degree of reproducibility of the estimates made by each technique, a reproducibility which is reasonably good as Table I shows.

The third population was constructed with a restriction of the randomisation of the points: 336 equally spaced intersections were chosen on a square grid, and around each of these a point was allotted a position within a circle of radius half the distance between the intersections. Within these circles the positions of the points were chosen strictly at random by choosing the bearing and distance from the intersection with the aid of the random-number tables. By this means a population was obtained whose members were dispersed more evenly over the ground than in a random dispersal, simulating under-dispersion. Whereas the balance of evidence favoured the Craig calculation in the grasshopper experiments, the empirical trials come out strongly in favour of the Clark-Evans formula. The known values in these instances lie between the adjusted and unadjusted Clark-Evans estimates.

The effects of under-dispersion seem to be of little importance, to judge from the empirical trials reported, but one cannot safely dismiss the possibility that grouping (over-dispersion) is partly responsible for the superior performance of the Craig model in the English, and to a lesser extent the French, trials in the field. Perhaps a few copulating pairs has a different influence on the differential sensitivity as compared with the type of aggregation that gives rise to negative binomial and similar sampling distributions.

Discussion

The following points of interest emerge from this preliminary enquiry. Firstly, nearest-neighbour measurements can give useful supplementary information about animal population estimates, although the existence of two distinct bases for the computation, leading to estimates which differ by a factor of 4 or thereabouts, is unsatisfactory. Where the conditions are such that the basic assumptions of the Clark-Evans approach are realized, as seems to be the case in phytosociological sampling, this form of computation is naturally preferable, but in the experiments reported here the conditions of Craig's form of computation may be nearer those which obtain in the field. Craig's approach, which has been ignored by subsequent writers, does not seem to be less plausible theoretically, and the simplicity of that used by Clark

and Evans, and by subsequent workers, may be deceptive.

Generally, these nearest-neighbour methods may be used to investigate density if random dispersal is assumed, and randomness if the density is known. However, very little is known about the sensitivity of these methods to different kinds and degrees of non-random dispersal. This investigation does suggest, however, that verification of the extent to which the initial assumptions of the method are satisfied in any particular type of experiment may need to include a wider range of considerations than randomness, since it appears that the quantitative effects of non-randomness are small compared with the differences between population estimates based on the mathematical models of Craig and of Clark and Evans.

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A SIMPLE CHEMICAL LIGHT-METER[1]

The property of anthracene ($C_{14}H_{10}$) in benzene solution to polymerize into insoluble dianthracene ($C_{14}H_{10})_2$ on exposure to sunlight can be used to measure the amount of light that enters the habitat over a period of time. As the technique is simple and the materials inexpensive, the method should have considerable practical value in certain types of ecological studies. Summation readings can be obtained for periods of a few hours to a day or two, simultaneously in several places or in various niches of the habitat. An electric power supply is not needed and there is little danger of damage from the weather or from animals; readings may even be made in underwater habitats.

A saturated solution of anthracene is made by dissolving an excess of the crystals in benzene (benzol) at room temperature. The solution is filtered, then diluted slightly to prevent supersaturation should a change of temperature occur. The particular concentration is not important as long as a control is kept for comparison.

The solution is placed in screw-cap vials with foil-lined bakelite caps. The capacity of the tubes is not important but in comparative tests all tubes should be of uniform size and quality of glass. They should be filled completely with the solution. A number of tubes can be made up (in ordinary room light) and stored in a light-proof canister until ready for use.

The anthracene tubes are placed out in the habitat, on the ground or supported in a horizontal position at any particular level in the plant canopy. As exposure to light proceeds crystals of dianthracene will start to form, then increase in quantity. According to the degree of exposure, the amount of crystals in the tubes will be seen to vary but it would be a difficult matter to judge the amount accurately by sight, or indeed by the ordinary field or laboratory methods since the crystals are often scant and variable in texture and some may adhere to the glass. However, for purposes of measurement the dianthracene may be disregarded and the analysis made on the amount of unconverted anthracene remaining in solution. With a spectrophotometer this analysis can be made quickly and accurately. The exposed tubes, then, are returned to a canister and held until they can be taken to a suitably equipped laboratory for reading.

As an example of the use of the technique, the following data from a test experiment may be given. Four 50-ml vials of anthracene solution were placed in each of five trays, one of which was left open and the others covered respectively with one, two, four, and eight layers of cheesecloth. The trays were then placed out in sunlight on a table (Fig. 1). One vial was removed from each tray at intervals of three, four, five, and six hours.

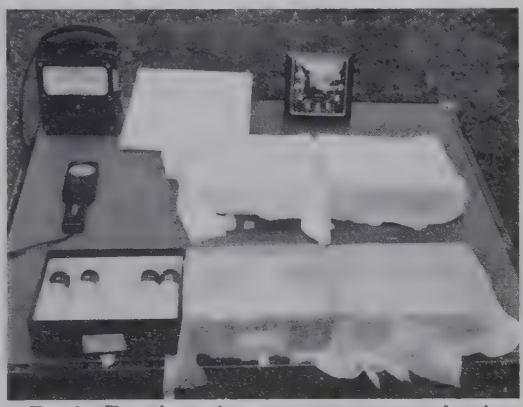

FIG. 1. Experimental setup to test response of anthracene solution to sunlight intensities as controlled by various layers of cheesecloth: front row of trays, l. to r.; no cloth, one layer, two layers: back row, r. to l. four layers, eight layers.

For comparison, readings in foot-candles were made at 5-minute intervals with a Weston Illumination Meter (Model 756 with quartz filter), its target being placed horizontally on the table adjacent to the trays. At ten random periods, the target was inserted in the trays through a trap door to determine the intensity under each thickness of cloth. The relative intensity in the open paper-lined tray was found to be slightly greater than on the table top.

TABLE I. Anthracene remaining in solution in benzene after various exposures to sunlight of graduated intensity produced by increasing layers of cloth. Relative intensity is indicated by *ri*

Exposure period	Foot-candle hours (*ri* = 100)	Anthracene Concentration (gm per liter)				
		no cloth (*ri* = 101)	1 layer (*ri* = 82)	2 layers (*ri* = 65)	4 layers (*ri* = 46)	8 layers (*ri* = 30)
3 hours	13,000	2.15	2.65	2.70	2.78	3.08
4 hours	23,000	1.38	2.15	1.90	2.35	3.00
5 hours	32,500	1.08	1.38	1.55	2.05	2.50
6 hours	40,500	.90	1.15	1.45	1.85	2.45

The amount of anthracene still in solution in the tubes at the end of the test was measured on aliquots of the filtered solution transferred to the cell of a Bausch & Lomb "Spectronic 20" colorimeter set at a wavelength of 350 mμ. Table I gives the anthracene concentration in each of the tubes. The figures show that as length of exposure to sunlight increases or as intensity for the same exposure period increases, less anthracene remains in solution on its conversion into the insoluble dianthracene.

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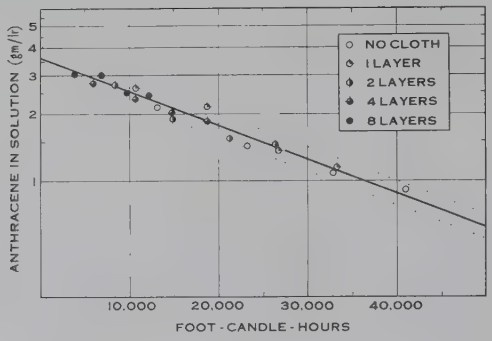

FIG. 2. Relationship of anthracene concentration (log.) in tubes to light exposure. The regression line and its 95 percent confidence limits (dotted lines) are computed from the combined data in Table I.

As the solution becomes weaker in anthracene the conversion falls off according to a logarithmic curve. A straight line is therefore obtained when the values are plotted on semi-log paper (Fig. 2). In the test all values save one fell within the 95% confidence limits in the regression analysis. Such a line may be used in other tests to read off light intensity once the concentration of anthracene in the exposed and control tubes is known, provided a similar technique is followed; vials of smaller bore, for example, provide a steeper line.

From preliminary tests under various plant and artificial canopies the anthracene tubes seem to have adequate sensitivity for light quantities between about 3000 and 50,000 ft.-cd.-hr., limits seldom exceeded in an ordinary day's sunlight. They may be of particular value in studies of conditions under the broken canopies of trees or crop plants where a number of tubes would be placed on the ground to obtain the diurnal light pattern at much less expense and trouble than by the conventional methods now in use.

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EFFECTS OF OVERGRAZING ON THE GRASSLANDS OF THE WESTERN GHATS, INDIA

Overgrazing might be defined as an intensity of grazing that so modifies the plant cover that its productive capacity is seriously impaired. It cannot be defined in absolute values but only in terms of degree. In its less pernicious aspect it might result merely in deleterious change in the botanical composition while in its extreme form the vegetative cover might be so depleted that soil instability and serious erosion follow.

In his classical monograph on succession Clements (1928) regarded the biotic formation as an organic unit comprising all the coexistent species of plants and animals in a particular niche. Both plants and animal react upon habitat and produce succession.

Daubenmire and Colwell (1942) made a very significant study of the effects of overgrazing. They assessed the type and extent of edaphic changes brought about in the Agropyron-Poa prairie association of South-Eastern Washington due to overgrazing.

According to Tansley (1936) anything like a careful study of the ecology of a plant community includes a study of animals living in or feeding upon it for animals have far reaching effects on the vegetation.

In the present investigation an attempt has been made to study the effects of overgrazing on the botanical composition and the edaphic factors of the soils of three regions, namely (1) Bombay (2) Khandala and Lonavla, 78 and 81 miles, respectively, south east of Bombay and (3) Talegaon, 96 miles south east of Bombay. Each region differs from the other in altitude and precipitation. Bombay, at sea level, has 80 in. of rainfall; Khandala is 1790 ft. in elevation and has 187 in.; Lonavla, at 2036 ft., receives 170 in.; and Talegaon, at 2025 ft. gets 30 in. of precipitation.

THE EFFECTS OF OVERGRAZING ON THE BOTANICAL COMPOSITION OF GRASSLANDS

Under Indian and other similar tropical conditions, the grasslands are semi-natural and are now regarded as a stable sub-climax formation.

The dominant grasses in Bombay are *Themeda triandra* and *Pseudanthistiria heteroclita*. Other associated plants are *Ischaemum ciliare, Crotalaria filipes* and *Smithia sensitiva*. Overgrazing in this association leads to the extermination of the dominant grasses and prevalence of *Eulalia fimbriata*. As the intensity of pasturing increases the latter is succeeded by *Eragrostis unioloides*. Simultaneously with the regression of vegetation, the soil is also washed off resulting in rocky and stony ground fit only for the establishment of useless weeds such as *Blumea eriantha, Bonnaya brachiata* and *Boreria stricta*. Other denizens of this regression stage of the vegetation are *Striga lutea, Sopubia delphinifolia, Rhamphicarpa longiflora* and several other Cyperaceae.

The dominant grasses of the subclimax at Khandala and Lonavla are *Arthraxon meeboldi* and *Heteropogon contortus*. Others associated are *Ischaemum ciliare, Smithia setulosa, Alysicarpus belgaumensis, Smithia sensitiva*, and *Desmodium gyrans*. On overgrazing, very hardy grasses like *Eragrostis unioloides* predominate. Further overgrazing of the vegetation at this stage leads to the maximum regression of the ground cover and erosion becomes inevitable rendering the habitat sandy, rocky and stony. *Blumea eriantha, Peltophorus divergens*, and *Murdania semiteres* establish themselves.

At Talegaon the lacunae of the thorn Scrub forests of *Acacias* are luxuriantly clothed with grasses like *Themeda quadruvalvis, Thelepogon elegans, Sehima nervosum* and *Themeda triandra*. Other associated plants are *Alysicarpus pubescens, A. tetragonolobus, Crotalaria filipes* var. *trichophora*, and *Indigofera trifoliata*. When these pastures are grazed they are replaced by hardier grasses like *Dichanthium annulatum, Andropogon pumilus*, and *Dichanthium caricosum*. Indiscriminate grazing and trampling at this stage results in the maximum regression of the vegetation, the main plants being *Gracilea royleana, Lophopogon tridentatus, Aristida redacta*, and *A. funiculata*. During the monsoon the productive layer of the soil is washed away rendering the habitat stony and permitting weeds like *Blumea eriantha, Pulicaria wightiana* and *Glossocardia linearifolia* to invade.

Given due protection from grazing by fencing in all the three regions mentioned above, the original subclimax could be restored if erosion has not gone too far.

The Effect of Overgrazing on the Edaphic Factors

The course of vegetational regression resulting from overgrazing native prairie has been described for many regions. Relatively little effort has been made, however, to carry these investigations far enough to include those subsequent changes in the soil, which follow the changes in the vascular plant population. By providing an understanding of the nature and degree of soil deterioration, investigations in this field may be of material aid in the program of range management and restoration. Furthermore, from the theoretical point of view, such studies cast light upon the vegetational influence, i.e. the degree to which a plant association determines its own environment.

Table I. The effect of overgrazing on the mechanical composition of the soil

Soil No.	Condition	Place	Mechanical Analysis			
			Coarse sand %	Fine sand %	Silt %	Clay %
1	Cut and Grazed Soil	Talegaon	2.48	7.98	20.20	69.17
2	"	"	3.17	10.83	27.88	50.13
3	Overgrazed Soil	"	49.14	26.33	10.85	8.35
4	"	"	22.01	6.29	18.82	36.07
5	Cut and Grazed Soil	Bombay	17.28	30.04	16.83	19.13
6	"	"	19.39	33.69	22.56	13.72
7	Overgrazed Soil	"	52.90	15.83	11.62	16.22

The pernicious effects of overgrazing are discernible both from the physical and chemical factors of the soil. From Table I it is evident that the mechanical composition of the soil is greatly altered by overgrazing and trampling. The clay content, which forms the bulk of the colloidal complex of the soil and from which nutrients are available to plants, have relatively high values in the "cut and grazed" regions (in which the grasses of the pastures are cut at the end of the monsoon and the cattle allowed to graze on it for one month at its beginning and one month after cutting) ranging from 50 to 69% whereas in the overgrazed regions (in which the grasses of the pastures are subjected to intense grazing throughout the year) it is considerably lower, ranging from 8 to 36%. Conversely, the soils of the overgrazed regions are sandy. This is due to the depletion of vegetation by overgrazing resulting in bare areas which exposed to rainfall bring about serious erosion of the clay portion.

Simultaneously with change in the mechanical composition of the soil, the moisture content also shows variation. As will be seen from Table II the moisture content which is on the average 7.15% in the "cut and grazed" region of Talegaon registers a decrease to an average of 3.30% in the overgrazed region.

From Table II it will also be clear that the chemical factors of the soils are also affected by overgrazing. Thus the organic matter content which ranges form 2.06% to 2.67% in the "cut and grazed" soils of Talegaon, becomes low in the "overgrazed" soils where it ranges from 1.14% to 1.20%. Similar trends in the organic matter of the soils have been found in other places, namely Lonavla-Khandala and Bombay.

The base exchange capacity which ranges from 47.3 to 53.0 m.e.% in the "cut and grazed" soils of Talegaon, show an alarming decrease in the "overgrazed" soils where the values range from 28.7 to 31.0 m.e.%. Likewise, the total exchangeable bases and the exchangeable calcium become consistently low in the "overgrazed" soils as compared to the "cut and grazed" soils in all the three places as evidenced from Table II.

Summary

The essential consequences of overgrazing in Indian pastures are (1) deleterious modification of the botanical composition, cover and yield, (2) alteration in the mechanical composition on the soil to a sandy condition, and (3) decrease of the moisture content, organic matter, total base exchange capacity, total exchangeable bases and the exchangeable calcium due to overgrazing and trampling.

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Table II. The effect of overgrazing on the edaphic factors

Condition	Place	Moisture Content %	Organic matter %	Total base exchange capacity m.e. %	Total exchangeable bases m.e. %	Ex Calcium m.e. %
Cut and grazed soil.....	Talegaon	9.27	2.06	53.00	48.80	31.80
"	"	5.02	2.67	47.30	41.20	31.00
Overgrazed soils.....	"	3.44	1.20	28.70	27.20	14.30
"	"	3.17	1.14	31.00	28.00	12.00
Cut and grazed soil.....	Khandala	3.94	7.93	26.90	25.40	12.40
"	"	4.11	5.17	16.00	15.40	10.60
Overgrazed soil.....	"	2.03	3.10	14.70	8.20	3.80
"	"	3.68	2.69	17.20	12.20	5.30
Cut and grazed soil.....	Bombay	6.12	5.06	33.50	28.50	18.20
Overgrazed soil.....	"	2.10	2.06	28.00	21.80	9.40

A DEFINITION OF ECOLOGY AND SOME THOUGHTS ABOUT BASIC CONCEPTS

The Definition

Three years after introducing the conception "ecology" in 1866, Haeckel defined it as "the entire science of the relations of the organism to the surrounding exterior world, to which relations we can count in the broader sense all the conditions of existence. These are partly of organic, partly of inorganic nature." Herewith Haeckel meant autecology; the notion "community" or "biocenosis" did not yet exist. But Haeckel may have had some prescience of it when he added a second definition, that of the "household of nature." This second definition is, in my opinion, appropriate neither for ecology nor for biocenology, though some German authors hold to it; it does not express the fact that ecology is a branch of biology; it could perhaps be a definition of the biology of living mass production, but as a definition for the whole of ecology it must be declined, even if changed to "the household of living nature." One may conclude that according to this strange definition the idiobiology, the biology of the single organism, apart from its environment, had to be the science of its household. This would be its metabolism and nothing more.

Later definitions in general have very little or not surpassed the first one of Haeckel. Out of the abundance of definitions very similar to that of Haeckel and to one another, two may be mentioned. King and Russell (1909) named ecology "the study of the relations between animals and their environment, both animate and inanimate." Eggleton (1939): "the science of the interrelationships of organisms and their environment." Definitions of this kind do not cover biocenology. Authors who are quite aware of the fact that ecology in its broadest sense is something *above* the branches of biology (like general biology, genetics, pathology etc.) have taken that into account by thoroughly changing the definition, so Elton (1927): "Ecology is scientific natural history," and R. N. Chapman had a similar view of it. While some of the students of ecology endeavour to keep the conception ecology as narrow as possible, in a specialist's manner, confined to botany or zoology, there is, on the other hand, a trend to expand it very far, in an universalistic manner, even beyond the limits of biology. Thienemann (1942) discerned three steps of bioecology: autecology, biocenology and a third one, which he named holography. On the holographical step the inorganic environment becomes more important than on the former steps. In these we are interested in relation to life only, in the third step the inorganic becomes an equal object of inquiry aside from its relationship to life. In this way biological branches melt together with branches of inorganic natural science. Limnology (and perhaps marine ecology too) is just as much hydrography as hydrobiology; both are united in it. There is a kind of soil science, forwarded especially by H. Franz, which is just as much ecology of life in the soil. The same trend to expansion exists in numerous inquiries about plant protection against noxious insects, inquiries including the whole biocenosis. In this way a certainly desirable "science of nature" originates; so I have named it (1937) in contrast to "natural science," which is a sum of branches. Elton presumed it with his definition "scientific natural history." Many naturalists concerned with ecology are still inclined to reject this development, but it is *not a proposal, it is an existing state of affairs.* Natural science is going this way to an unity above the single branches, without prejudice to their own life in any way.

The question is, whether all this can be named ecology. In holography, the inquiry on the environment is no longer an auxiliary science, but has become something just as near to the aim of the explorer as the inquiry of the life of the community. In this way, ecology has ceased to be a synthesized branch of biology, composed with the addition of auxiliary inorganic sciences; it has become a *viewpoint.* This viewpoint is not alien to almost all other science[1] or practice, e.g., to medicine in climatology, epidemiology and hygiene, and to law when in Mediterranean countries a homicide is judged more indulgently, if at the time of the crime the sirocco was blowing. Ecology, realized in three steps, has thus three meanings of different but coinciding extent.

Certainly "bioecology" (Clements) as a synopsis of animal and plant life with their whole environment is a synthesis of almost all biological branches in the sense that many or most of their questions arise again in ecology and gain in it an additional meaning, their true meaning, lying in the undivided, manyfold reality of nature. This is the very essence of ecology.

If in this way the scope and significance of "ecology" is clear, an adequate definition is possible. It has to express mainly the fact that ecology has to do with *complexes* in a great complex, the cosmos of life and environment, not simply with the sum of the relationships therein. Therefore I define ecology as *the science of the superindividual complexes* or if you prefer: as *the science of the living beings as members of the whole of nature.* Both these definitions are not new, but entirely neglected because they were given occasionally only, hidden in books which are not explicitly ecological, namely in the books of H. Dotterweich (1940) and F. Doflein (1914), the titles of which are cited below in the bibliography. Their definitions are the same. A third possible fashion of the definition is: *The knowledge of the complexes of life and the other environment.*

Even the individual with its environment is a superindividual system (or "life unit" of Thienemann), an "ecosystem" as defined by Evans (1956) who very correctly extended the term "ecosystem," which earlier pertained to the system of community and environment, to all superindividual systems, in accordance with the logical sense of the word. Other examples of the conception "superindividual complex" are: "parasite and host, and the community or the same with its environment." "Superindividual complex" is identical with the "ecosystem" of Evans, but the first is at the same time a declaration of the term "ecosystem." Thus the definitions given above cover the whole range of ecology. A German translation of ecology, namely "Umweltlehre," is in itself the shortest definition, meaning: science of the environment, a possible nomenclature, because "environment" presupposes a living being, to which the environment refers. That is enough concerning the definition.

The limit to *geography* has never been sharp, for ecology deals sometimes with landscapes (the biome with its environment!) like geography. But the latter does not go into detail so far. Biogeography was logically designed by R. Hesse as a part of ecology. Practically it goes its own way but overlaps with ecology. In botany ecology is even considered as a part of plant geography, or was so.[2]

[1] No wonder therefore that cytologists begin to see the life of the cell in a light like that of ecology.

[2] For more see Friederichs 1957.

The Two Meanings of "Sociology"

In botany the so called "sociology" of plants is a generally used conception. though, as E. Rübel (1920)[3] has stated, "die hier in Frage stehenden Erscheinungen mit Soziologie nichts zu tun haben." So it has come that sociology (in biology) has two different meanings. The name is appropriate for the science of the social relations of animals, the real "societies" (bee colony, fish school, bird flock). In the plant kingdom I cannot find cooperation analogous to that of animals. The historical development of botany led to an understanding of "sociology" as a pure science of order, of the spatial relations common to groups of plants. If this direction of inquiry is seen as something aside from ecology, this conception is centrifugal but not incorrect. On the other hand, this "sociology" can be conceived of as ecology, as the first and lowest step of biocenology, because the spatial relation to different habitats and of the plants to one another are ecological relations, and because this inquiry refers inevitably to other factors of the environment too.

I believe the reason for this historical development, besides the existence of plant geography anteceding that of ecology, is the fact that the interspecific relations of plants seemed to be rather poor, compared with the richness of such relations among animals. This is in spite of the frequency of parasitism and symbiosis among plants, of competition of roots, and competition for light and nutrition. But besides the "allelopathy," known since the time of Molisch, there seem to exist *many* chemical influences of plants upon one another in form of root secretions and bacterial and fungal action, influences which work antibiotic or "probiotic." With exception of the protophytal actions, the knowledge of such influences is still in the embryonic stage, and to cite literature about them would lead too far. In every case the interspecific actions of plants are much more manifold than was realized when plant sociology originated. At that time the common habitat seemed to be the most important interspecific relation unifying the plants into "societies." Animals have in general not so firm a spatial connection; their interspecific relations are striking and stand in the foreground.[4] The double signification of the word "sociology" is so commonly used that one must be resigned to it.

The Community is not an Organism

Another point worthy of further consideration is the still repeated idea of the community or the ecosystem of both the community and its inorganic environment as an "organism."[5] This idea has shown itself very productive in the early days of biocenology and it is of didactic value in practice, but it cannot stand a careful examination. It has long been demonstrated, first perhaps by the author (1927, 1930), later especially by Remane (1939, 1950) that the ecological units are something else than organisms. But the idea has durability, and therefore the many and convincing arguments against it may shortly be resumed.

First, what is similar in the both of them? They are stationary energetic systems. Stationary means unsteady but enduring in all change of the strength of their acting components; the changing strength of them is the fluctuating number of the individuals of every species. The members of the community are more or less dependent for their existence on the whole, from the functions of the other members, as the members of a living organism are. The community together with its habitat develop by succession to a climax in a manner comparable to the development of an organism; such directiveness however is a quality of many inanimate open systems too, hence not characteristic for life. The same statement is valid for selfregulation, proper to open systems of both animate and inanimate nature. But here already the great divergence begins. The community has not, as an organism, a regenerative power. A lost species of the community cannot be regained within the ecosystem; it can come back from outside only.

If we compare the community to the superorganism "bee colony" and the different species of the community to the single bees, then we ascertain that the bees *cooperate,* as do the parts of an organism. The different species, united in a community behave themselves otherwise; each of them has its own innate laws; they cooperate relatively little (symbiosis etc.); in general they work against one another though the result of the whole of their interrelationships guarantees the existence of all the species under the given conditions.

2) The living being is a real whole, a "gestalt." That is to say, it has qualities and functions which cannot be declared and understood out of the qualities of the parts (especially the soul-life). Such qualities of the community are not known.

3) A further deciding difference, emphasized by Remane, is that the community, when it is beginning anywhere by settling in new land, is formed by and by, because the different species, which are the potential members of the community, reach the new habitat by and by incidentally or on purpose, the presence of definite organisms being condition for the settlement of others, e.g. the presence of plants for animals, etc. In this way the community is formed. The organism on the other hand, begins as a primary whole[6] and differentiates itself into its members. Thus the community cannot reproduce itself as a whole; the organism does. As Schubert-Soldern put it, "The organism is hologene, the community is merogene."

4) In the organism almost every process of life is directed sensefully. There is little room for chance; the life processes are directed by the order of the whole. In the community too they are often directed, e.g. by the activity of a predatory animal in relation to its prey, and by all the numberless purposive actions of animals and directive reactions of plants. But whether the predator meets his prey at all, depends more or less on chance. In the community as in the organism, the whole has an influence upon the members because of the general web of life, but chance plays a great role in the ecosystems and affords much senseless destruction by hunger, drought, cold, and the order is maintained by the struggle for life. *The ecosystem has another, a looser form of order than the organism* which is incomparably more integrated.

In view of the differences and the similarities it is possible to speak, as does Tansley, of a "quasi-organism." But that is a lame compromise, the character of community and its ecosystem with the habitat can be expressed more exactly, as did Thienemann, with the term *life-unit* (Lebenseinheit), namely life united with life to

[3] See also E. Schmid (1922).

[4] It happens that zoologists work in the same manner about "societies of animals"; for names of authors see Friederichs (1957).

[5] Repeated, for example, by Taylor (1935), by Clements and Shelford (1939), by Allee, Emerson, Park, Schmidt (1949), by Carpenter (1939) p. 85.

[6] There are some exceptions; see Remane 1939.

an ecosystem, or life with environment. I proposed to classify the category to which those ecosystems belong, by the word *"organization,"* remembering that degree of affinity to the organism which exists really, and at the same time remembering the "organizations" of the human society.

The Niche* and Life Zones

The next terms which have to be considered here, are "niche" and "life zones." The niche in its present refined meaning is the abstraction of the indispensable conditions of life, the special needs of a species, often created in part by the animal or plant itself which is the beneficiary of the niche, e.g. the mole of its channels and holes, the plant of the crumbling structure of the soil in which it roots. Only the *immediate* necessary environment is meant by "niche," though indirect relations conditioning the direct ones are just as indispensable for life, e.g. for the dung beetle not only the dung but also the cow or sheep, for they deliver the dung! Some people[7] are willing to extend the conception "niche" so that the owner of the niche is included. K. Günther says that the niche is not simply a complex of conditions given in nature, but on the other hand characterized by the needs and the behavior of the organism which uses it. In my opinion that is self evident; the owner of the niche is the complemental concept to it. Therefore it cannot be included in the conception "niche"; this inclusion would annihilate the concept "niche"; the niche is a part of the surroundings indispensable for the life of this species, and not more. The meaning of the term "niche" has been extended since the first incomplete definition by Elton, but logic forbids extending a concept by inclusion of its complement. However, in the conception of those authors, the niche is not simply given; the animal or plant which takes possession of it, adapts itself and modifies the niche in accordance to its needs. One can say: The living being in question finds certain circumstances in the exterior world and out of these given conditions it makes a niche. Plants, of course belong often to the factors composing a niche for an animal, and animals can belong to the niche of other animals.

For example of the species of birds invading the cities and settling there with predilection, in middle Europe the blackbird and the magpie have extended and changed their range. The niche "garden," predicated by the blackbird, is not simply characterized by the abundance of food available there for the birds, but also by the fact that these birds have not made use of this possibility of life in such an ample degree until the last century, and that, in doing this, they have changed their behavior considerably. On islets of the North-Sea, crows build their nests on the ground, for there are no trees. This is adaptation to conditions which lie at the frontier of the amplitude of reaction of the animal. Besides that, this behavior may be, as it were, an invention, an intellectual action of these clever birds. Thus they have *made* the islet a niche for themselves. Günther means probably this relation to the environment, and in this respect he is right. But concerning the inclusion of the possessor of the niche, we may compare the consequence for the analogous case of the relation of organism and its next environment. According to the principle applied to the niche, the environment would be the part of the surroundings, connected with the living being in question, *together with this organism itself*. Certainly they condition one another; the concept environment presupposes the individual and no individual exists without environment. Logically however they are *complements*.

Just the same has to be said about the manner in which "life zones are sometimes understood. A life zone is the sum of the common or similar niches of a multitude of animals with the same form of life, e.g. of the small singing birds or of the small fossorial mammals. Such groups of animals are characterized not only by a common form of life but by organization—traces too, common with little variability to them all. The same authors who use the term niche too broadly, do so with life zones; they want to include the animals or plants characteristic of them. This complement to the notion "life zone" could be called "group of convergent species," for they converge in evolution, gaining a similar form of life together with certain common traces of organization.

The Concepts "Stabiliment" and "Organoid"

If the animal itself brings its immediate environment partly in form, as the mole does, or creates it, as the bird, building a nest, the spider, constructing a web, and the bees, masoning the combs, obviously this part of the environment is distinct ecologically from the world around. It is not always the "home," constructed in this way; it can be a tool (a secretion fastening a sessile animal to its substrate or a cover for protection, as the spun cover of a chrysalid). Such parts of the environment I named (in a book of 1955) the *stabiliments;* they stabilize the life of the individual constructing them and its offspring. Besides that, other species often profit from stabiliments, which they have not made themselves, e.g., if a wasp occupies the abandoned nest of another one as certain tropical species do.[8] In the case of man the whole apparatus of civilization is stabiliment. The plant does not create stabiliment for itself as a single plant, it creates it for the plant community, e.g., the litter of the forest floor and the humus.

There is still something between the exterior world which begins with the stabiliments, and the very life in centre of an individual ecosystem—the inanimate parts of the organism which can be discerned just as in the cell the paraplasm can be distinguished from the protoplasm. Inanimate parts of the body, not able to reproduce themselves and to function by own activity, are exoskeletons of crabs or insects, claws, nails, the walls of the plant cell, and the brown shell of an onion. All such parts of the body are products of animate parts of it; they are not organs, for they do not function actively; I call them *organoids*. It can happen that they become stabiliment, when the body gets rid of them, as, in the case of the fly pupa, the shed integument of the last larval stage becomes the pupa's case.

Organoids are in general solid stuffs retaining their form a long time after death; stabiliments do the same after death of their constructors. So organoids and stabiliments are that which remains (or can remain) as sediment. So they form whole geological layers, e.g., limestone or mineral oil, for fat belongs to the organoids.

The Holocene

Now we come to the most important question of *the*

* The term "niche" as here used is quite different from the definition given in the 1952 Report of the Committee on Nomenclature, Ecological Society of America. "Life zone" is also used in a different sense from that familiar in this country.—Ed.

[7] See K. Günther, F. Peus and some others.

[8] *Odynerus hildebrandti* after *Eumenes maxillosus,* and *Sceliphron violaceum* after *Sceliphron hemipterum* in Madagascar. (Friederichs 1918.)

ecosystem unifying community and habitat. Is there such a system and how can it be named best? If it exists as a system, it postulates that habitat (biotope), phytocenosis and zoocenosis coincide topographically. Nobody has any doubt that the frontiers of a plant society depend upon the physiographical factors of the place, that is, the habitat,[9] where man has not disturbed this natural relation of the two. Whether the frontiers of an animal community coincide with a coordinated plant community may be still controversial in American ecology,[10] in Continental ecology it is rather not. The first observation already shows that there are a lot of characteristic species of animals in every part of the landscape, corresponding to definite plant communities, e.g., animals of the coniferous forest, the deciduous forest, and all forests, or to the moor, the prairie, the flowing water. Mainly on the ground of quantitative inquiries, many ecologists came to the conclusions that plant and animal communities coincide in area as far as the locomotion of the animals permits it.[11] In bioecology plant and animal "communities" are pure abstractions; concretely there is only the biotic community, composed of them both, and they depend upon one another, the animals more upon the plants than conversely. The community needs them all for its existence—the producents (green plants), the consuments (animals) and the reducents (protophytes).[12] The question of the coordination of more or less definite species in combinations of animals or of different quantities of individuals of them to definite plant-combinations could be considered as settled as a right observation. But this controversy shall hardly ever end; the personal decision of the explorer depends upon the observational and conceptual order (Whitehead) of his mind. The more analytic mind shall always be inclined to dissolve the biotic community into the abstractions phytocenosis and zoocenosis, and there to stop his inquiry; the more synthetic mind shall see it as a concrete unit not only in the start of his inquiry but again at its end, after analysis.

If that is so, then the question arises: how should we name the unit of the biotic community with its habitat? Some authors extended the concept biocenosis to this whole ecosystem[13] and this view has been renewed recently.[14] The mistake is again (as in the niche) that the complements are confused with one another. Aside from the fact that there are many reasons to oppose them to one another, the fact has to be considered that the environment of a community, consisting of the physiographic factors, is reason for many common traces of the different life in it, and the most extreme factor determines the character of the community. A practical reason is that a forester or a farmer planning the land-use has to distinguish, of course, between the land and the kind of plants and other life to be settled there. This is a trivial statement, but one sees that it is not verified where the notion habitat is suppressed. Many authors, following Elton, call the unit of community and habitat "ecosystem." Certainly it is such, but so is the unit of the individual with its environment and so is every part of the community with the coordinated parts of the community and the habitat. It was mentioned above that recently F. C. Evans has first recognized or published this general signification of the word "ecosystem." Thus, ecosystem is a category, not a term. Evans' proposal to discern "individual-ecosystem," "community-ecosystem" etc., is possible though not quite practical or well expressed.

But why not apply an existing univocal term? Long ago (1927) I introduced the term "holocene" or "cene" (in German "holocoen" or "coen") for the ecosystem in question and defined it as the combination of the ecological factors, both animate and inanimate, unified by their action and counteraction upon one another. I underlined the interrelations of all of them, the "web of life," forming the part of a landscape, which is called a holocene, to a whole, in which no one factor can change without affecting all others. This is the *holocenotic principle.* The statement that a change in any factor of the cene affects all the others, is a formal consequence of the "web of life." Today, I am aware that the principle has to be more restrained perhaps. But that may be considered another time. The principle means mainly that every action of an ecological factor is (formally thought) a function of the whole, and, practically at least, of many factors together (of their fluctuations) because of the interrelationships of them all, similarly as in an organism, but as a result of a looser order than in the organism.[15] The holocenotic principle was understood only scarcely at first and the understanding grew slowly. W. D. Billings made (1952) a principiant analysis of the environment complex of the plant on the basis of the holocenotic principle.[16] This principle means that in the holocene everything acts directly or indirectly on everything else, though the more distant relations are not apprehensible and practically negligible. As far as they are apprehensible, the special environment reaches. Billings wrote: "The holocenotic principle is fundamental to any understanding of environment-plant relationships. Complete explanations of ecological phenomena are not possible without it." Billings ascribed the authorship of this principle to Allee and Park (1939). These authors used and named it as a scientific fact of already anonymous origin, though it was not generally fully recognized.[17]

[9] In German ecology the English "habitat" is named "biotope"; "habitat" is then the substrate, living or not, where an animal or plant can be met regularly.

[10] See Carpenter 1939.

[11] W. P. Taylor (1935) names a long series of authors who have pleaded for the biotic community as comprising plants and animals in the same area. Furthermore I. Braun-Blanquet in his classical work "Pflanzensoziologie" (2. ed., 1951) consents to that conception and enumerates many authors who are of the same opinion. Here can be added P. Palmgren (1928), H. Franz (1943), W. Kühnelt (1944, 1951), B. Heydemann (1955), for Collembles H. Gisin, for birds H. Bruns and other authors, named by Bruns.

[12] A. Thienemann (1942). The identification of producents with the green plants, of the consuments with the animals and of the reducents with protophytes is a simplification. Things are much more complex; and certain categories of communities contain no green plants, especially in the deep sea and in caves.

[13] Tansley (1935) according to Carpenter, p. 75, Allee 1934 according to the same, but later he spoke of the holocenotic principle.

[14] W. Schwenke.

[15] The unity of nature as a causal factor is emphasized in the introduction of a paper of Burr and Northrop (1935, see especially p. 325 near the end).

[16] See also S. A. Cain 1944.

[17] The holocenotic principle and its development and bearing would be better known, if in 1928 an American journal had not declined an article of mine, on the grounds that the holocenotic principle was "not understandable for the average reader" (while at the same time I was teaching on the basis of this principle at the

I think, the term holocene, which for practical use in general can be abbreviated to "cene," is a handy one. It can be varied in several directions. For analysis of the holocene I recommended the distinction of *abiocene* (physiographical) and biocene (= biocenosis). The ecosystem of the individual or the species with its environment can be named *monocene*. F. Schwerdtfeger (1944) added the concepts *"gradocene"* and *"pathocene"* in the forest-epidemiology and -pathology.

A very important consequence of the holocenotic principle is that the whole of life on earth and its environment, thus the cosmos of life, is just a stationary equilibrial system as is the single cene, and that it forms the *great, all-life embracing holocene*—the *unity of nature*. In this way "nature," an abstraction before, becomes concrete and shaped, instead of a bewildering multitude of things, not understood "in the unity of thought" (A. V. Humboldt). Goethe and many illustrious geniuses before him had a presentiment or partial insight of the unity of nature; today, however, the idea has left behind it the philosophical stage; it has become a scientific fact that "nature" is a complex equilibrium (in the ecological sense of the notion). The holocenotic idea is very productive for the synthesis; it is the great synthesis itself and leads to a just interpretation and evaluation of the results of analysis. This recognized, a great number of problems can be solved out of it by deduction, or they vanish in the general idea. The number of possible controversies is restricted, for everything has a definite place in our idea of the whole of nature. Especially the hurly-burly of different concepts in ecology would be diminished by a real understanding and application of holocenotic thought. This is the inestimable value of every real synthesis. Bioecology is a synthesis.[18]

There are books on general ecology, devoted to the definition of the basic concepts, and it is in general nevertheless rather clear what is meant by the terms used there. But there is danger of confusion and avoidable controversies. A lack of clearness can lead to logical but false consequences. In another branch of science, physics, a warning example is that of the "ether" as a insufficiently defined conception. Much fruitless controversial discussion originated therefrom.

The questions treated in this paper are more fully dealt with in the journal "STUDIUM GENERALE."[19]

SUMMARY

Ecology is the science of the superindividual complexes of nature (life units or ecosystems) or the science of animals and plants as members of the whole of nature. For man's ecology the time has not yet come.

There are three steps, different not in kind, but in extent: (a) specialized ecology, (b) bioecology, (c) holography or science of nature. The latter step is characterized by ecology as a viewpoint.

The immediate environment is stabilized by structures made by intentional actions or by organic reactions of animals for themselves and by reactions of plants for the community. They are called "stabiliments." Still nearer to the very life of the organism, there are inanimate structures, parts of the body, products of the protoplasm, not functioning by their own activity, but passively. They are called "organoids."

Habitat, phytocenosis and zoocenosis coincide topographically. They form together an ecosystem, called holocene or cene. The farreaching consequences of this concept are exposed.

University of Minnesota). Indeed, the "average reader" had very little feeling for synthesis and for thinking from the view of the web of life (and just as little of the whole of the organism). And now? Little has been changed (See hereto Clements and Shelford, 1939, p. 2).

[18] W. P. Taylor (1935): "The emphasis placed by bioecology on organism and environment as a great unitary system is an inspiring one, and should lead to a more profound insight into many problems in diverse fields of human interest and larger contributions to human welfare." The same ideas see in publications of K. Friederichs (1930, 1937, 1957).

[19] K. Friederichs: Der Gegenstand der Ökologie (1957).

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FOG DRIP: AN ANTICIPATION OF ECOLOGY

Not infrequently the modern ecologist finds, in sources antedating the rise of ecology as a science, comments which presage the type of observation now a part of ecology. Whitford (1950) writes of Thoreau as an ecologist and points out how some of his ideas foreshadowed current ecological thinking.

Gilbert White in his classic, "The Natural History of Selbourne," published in 1788 makes many salient comments which are perceptive by ecological hindsight and at one point make striking parallels to the observations of Oberlander (1956) concerning summer fog precipitation in the San Francisco area. Oberlander notes, "Here a trail or road may be dusty dry through grassland and chaparral then suddenly bog down in mud and pools of water beneath tall trees. On the crests of ridges where there is no high ground above for seepage this summer fog precipitation is most striking. The wind blows fog against the branches of the tall trees on the ridge top where it condenses and drops like rain on the ground below."

White's book is a collection of letters on his natural history observations of his parish in England and one reads as follows:

"Selbourne, Feb. 7th. 1776

Dear Sir,—In heavy fogs on elevated situation especially, trees are perfect alembics, and no one that has not attended to such matters can imagine how much water one tree will distill in a nights time, by condensing the vapor which trickles down the twigs and boughs, so as to make the ground below quite in a float. In Newton Lane, in October 1775, on a misty day, a particular oak in leaf dropped so fast that the cartway stood in puddles and the ruts ran with water though the ground in general was dusty."

He goes on to comment upon the effect of leaf type upon the amount of water supplied and upon the effects of tree drip in keeping small ponds full upon the summit of chalk hills even during drought periods when ponds in the vales were dried up.

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A GRAVITY FLOW DEVICE FOR AIR SAMPLING

The following method is described for drawing air through an absorption fluid while at the same time measuring the air volume. Originally designed for analysis of atmospheric gas components, it may have wider adaptability in the growing fields of ecology, meteorology, and in air pollution and radio-contamination studies.

It is applicable where only small samples are needed and in situations where pumps and metering devices are not possible. A field unit for the same purpose is described by Lůndegardh (1924). Another, featuring meter and battery driven pump, was used by Wallis and Wilde (1957). The present has the advantage of simpler design, and can be constructed of ordinary laboratory apparatus.

The apparatus (Fig. 1) consists of two systems, one (A, B) removes the air component, and the other (C) pulls the air through the former. The removal system is essentially that of Böhning (1949), used for measurement of asmospheric carbon dioxide in photosynthesis studies. This system may be of any design specific to the problem at hand. It is essential only that the scrubber solution lie between the external atmosphere and that of the system both before and after the sample has been taken.

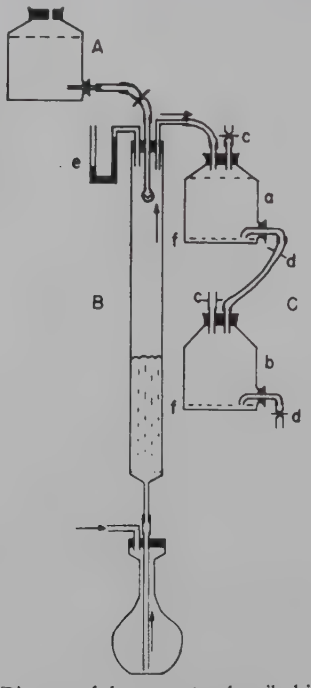

FIG. 1. Diagram of the apparatus described in the text. Arrows indicate the direction of air flow.

The component (C) is simply a gravity flow device with manometer attached.

Water levels in the bottom of aspirator bottles (a) and (b) are adjusted (as f) so that none drains from the outlets though the pinchclamps (d) are open. These clamps are then closed. A specific volume of water is added to (a). The desired scrubber solution is added to the volumetric flask. The upper clamp (c) is closed; the lower opened. The upper clamp (d) is opened; water drains from (a) to (b). Resulting pressure decrease causes the scrubber solution to rise into the tower, and a calculable volume of air passes through it. After drainage is complete, upper clamp (d) is closed and manometer (e) is read.

It will be found that the volume of air passing into the system is less than the water volume moving from (a) to (b) due to change in pressure. The air volume drawn (Vd) can be calculated as:

$$Vd = \frac{Vt \cdot Pi}{Pa} - Vt + Vw$$

where Vt is the volume of air space above the level of the scrubber solution, including space in bottle (a) above level (f) and other minor spaces; Vw is volume of water draining from (a) to (b); Pa is atmospheric pressure; Pi is internal pressure, Pa less manometer reading.

Upper clamp (c) is now opened to allow internal pressure to rise to atmospheric and fluid held in the tower to return to the flask. The tower is rinsed from source (A) and the solution or mixture in the flask is treated as desired.

Arrangement of fixtures on bottles (a) and (b) permit simple exchange of position to begin the next run. Or, if a larger sample is necessary the bottles may be switched and air drawn through the same scrubber solution.

Proper manipulation of the gravity flow device will pull air quantities calculable with an accuracy of three-tenths maximum, one-tenth average per cent error.

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THE DISTRIBUTION OF FOX POPULATIONS IN RELATION TO VEGETATION IN SOUTHERN GEORGIA[1]

The present paper deals with the distribution of gray fox (*Urocyon cinereoargenteus*) populations in localized areas and discusses food supplies of the major habitats as one of the many ecological factors which may be responsible for varying population densities.

Nineteen gray fox populations, located in 18 widely separated counties in Georgia, Florida, and South Carolina were evaluated by 51 censuses. These embraced 340 standardized census lines with 3058 trap stations. The census consists of trapping along primitive roads ran-

[1] This research was conducted under a grant from the National Institutes of Health of the U. S. Public Health Service.

domly selected throughout the areas to be checked. Each road selected was trapped for seven consecutive days with the traps set at 0.2 mile intervals (Wood 1954a).

The number of foxes caught in 7 days at each station of all trap lines was recorded. When a Poisson distribution is fitted to these data and the expected compared with the observed by Chi square, it is found that the distribution is not random (Table I). However, the number of stations catching zero foxes is not different from chance expectations. Hence the proportion of stations catching zero foxes can be used to compare densities in various places (Wadley 1954). In practice the percentage of stations that caught a fox is used because it is easier to visualize the relationship when a higher number (proportion) means more foxes. The standard error was calculated from $\sqrt{pq/n}$. In this paper percentage positive will mean the number of stations that caught foxes in 7 days multiplied by 100 and divided by the number of stations set in the area.

TABLE I. Distribution of 3058 trap station subsamples of Gray Fox census lines showing numbers of foxes captured

Foxes in 7 days	Stations	Expected	$\frac{(O-E)^2}{E}$
0	2468	2413.3	1.239
1	475	571.4	16.263
2	98	67.6	13.671
3	15	5.3	23.207
4	2	0.3	

$\bar{x} = 0.23675$
Chi-square = 54.380

The first problem to be examined is the variation of fox densities within areas such as counties and large estates. The results of several trap lines in each area were grouped and examined to see whether the different lines fell within expected limits. Table II combines all the censuses of an area into one entry and lists the area, the number of stations, the number of trap lines, the mean percentage of positive stations, the range of the percentages and the 5% confidence limits. In only one (Newton Co.) of the 51 censuses in the 19 populations checked was the range of the percentages positive of the individual lines within the 5% confidence limits of the census (mean ±2 SE). This somewhat crude procedure shows that the population of gray foxes is not evently distributed throughout the areas.

TABLE II. Gray Fox Census in 19 localities of Georgia, Florida and South Carolina

	Number Stations	Number Lines	Mean Percent.	Range of Percentage	Mean ± 2 SE	
Norias Plantation, Ga.	330	37	20.2	57 - 0	24.6	15.8
Edge Plantation, Ga.	254	23	10.7	40 - 0	14.5	6.9
Savannah River, S. C.	440	44	28.7	80 - 0	33.0	24.4
Wakulla Co., Fla.	150	15	24.0	50 - 0	31.0	17.0
Jackson Co., Fla.	94	12	28.0	66.7 - 0	37.3	18.7
Crisp Co., Ga.	160	21	14.2	40 - 0	19.7	8.7
Ben Hill Co., Ga.	84	14	22.3	50 - 0	31.4	13.2
Thomas Co., Ga.	485	56	11.7	55.5 - 0	14.6	8.8
Mitchell Co., Ga.	174	23	15.1	50 - 0	20.5	9.7
Colquitt Co., Ga.	159	20	20.5	80 - 0	26.9	14.1
Grady Co., Ga.	193	25	23.2	80 - 0	29.3	17.1
Mitchell Plantation, Ga.	97	6	20.6	30 - 10.5	28.8	12.4
Liberty Co., Fla.	70	7	7.2	20 - 0	13.4	1.0
Washington Co., Fla.	30	4	57.1	75 - 33.2	75.2	39.0
Newton Co., Ga.	31	5	30.2	40 - 14	46.7	13.7
Fort Benning, Ga.	70	7	10.0	30 - 0	16.7	3.3
Marion Co., Fla.	69	7	14.8	33.2 - 0	23.3	6.3
Putnam Co., Ga.	39	5	10.0	37.5 - 0	19.6	.4
Jackson Co., Ga.	50	9	40.1	57.1 - 16.6	54.0	26.2

In the Thomasville area the land use practices of the large plantations produce three major habitat types. These are (1) mixed hardwood and pine forests with dense underbrush (2) savannah pine lands and (3) small irregularly shaped fields dispersed among farm woodlands. The relative density of foxes in these three habitat types can be examined. These habitat categories are large and possibly quite unsuitable for workers considering species with small home ranges; but for foxes, which range a mile or more, this classification seems reasonable—at least in this area where the special management of the large plantations results in extensive areas of one type. In wooded areas with dense underbrush 32 census lines with 271 stations gave a percentage positive of 6.4 (SE 1.48). The 2464 trap nights in this habitat produced 24 foxes or 102.5 trap nights per fox. In the savannah pine lands 21 census lines with 181 stations gave a percentage positive of 15.4 (SE 2.68). The 2803 trap nights in this cover type produced 40 foxes or 70 trap nights per fox. In the areas supporting both cultivation and woods 26 lines with 274 stations gave a percentage positive of 22.1 (SE 2.39). The 1443 trap nights produced 82 foxes or 50.5 trap nights per fox. Although the latter two types do not differ significantly ($P = .06$) the trend seems apparent. These data resemble the trapping studies in Texas (Wood 1952) which also suggest that areas supporting a diversity of fields and woods are more desirable fox habitats than are large land areas of one type.

The reason for the uneven densities of foxes is doubtless due to many ecological factors. The effects of food supply are here discussed as one possible factor. To investigate this aspect, 171 gray fox stomachs were examined from the coastal plains of North Florida, South Georgia, and South Carolina. The foxes were caught over a five-year period (1936-1940) with a few added from 1952-1953. The analysis of the stomach contents was conducted at the U. S. Fish and wildlife Service, Food Habits Division, at Patuxent, Maryland.

It is realized that local abundance and annual fluctuations of food materials may affect the food eaten at any one locality during any period. It is felt, however, that a collection taken from a wide area over an extended number of years will tend to minimize the local abundance fluctuation and give a better insight into the staple foods of the coastal plains foxes. For obvious reasons no attempt is made to evaluate the abundance per se of the items found in the stomach.

The analysis of foods eaten is based on the annual and seasonal totals. Since the study is interested in the distribution of foxes as opposed to the details of a food habit study, only two seasons are considered—summer (April through September) and winter (October through March). This single division is used since a more refined break-down of seasons is unjustified here. Of course seasonal break-downs in a discussion of foods should consider periods of availability of the different kinds. Of the 18 foods representing 1% or more of the annual diet (Table III) only Rubus has a period of availability considerably shorter than the seasons here described, for the climate changes of this area have little effect on the availability of vertebrate foods and insect numbers are high from April through September. The

TABLE III. Foods eaten by gray foxes which comprise 1% or more of the seasonal or annual volume. (About 20% of the volume is represented by 70 different foods occurring in quantities of less than 1% of the total)

Food	Winter		Summer		Annual	
	A	B	A	B	A	B
Sylvilagus	50.0	66.8	24.6	31.6	29.0	37.0
Sigmodon	6.7	33.3	3.0	8.5	3.7	11.1
Peromyscus	tr	3.0	2.4	7.8	2.1	1.1
Geomys	3.2	3.0	tr	0.7	tr	4.7
Rattus	....	....	1.1	1.4	1.0	1.1
Galliformes	2.0	3.0	2.0	3.0	2.0	2.9
Colinus	2.6	6.7	1.8	6.4	2.3	6.4
Chicken	2.6	3.0	1.0	3.0	1.3	2.3
Fringillidae	tr	12.0	1.3	4.9	1.1	6.4
Diospyros	9.0	30.0	4.3	25.6	5.0	23.0
Peanut	11.0	23.0	1.4	4.3	3.2	7.6
Prunus	....	....	3.1	9.2	2.6	7.6
Rubus	tr	10.0	2.0	18.4	1.2	14.6
Orthoptera	tr	78.0	19.8	78.5	12.8	75.0
Coleoptera	tr	46.4	9.4	81.0	5.6	86.0
Lepidoptera	tr	22.7	2.4	36.0	1.7	41.0
Hemiptera	tr	9.7	2.0	24.0	1.5	21.0
Odonata	tr	3.0	1.7	8.0	1.0	4.7
Total Foods						
Mammal	62.6	....	35.9	....	40.0	....
Bird	8.9	....	7.7	....	8.1	....
Reptile and Amphibian	tr	....	1.6	....	1.4	....
Plants	20.6	....	13.4	....	15.3	....
Insects and Invertebrates	7.7	....	41.4	....	35.0	....

A=percentage of total volume represented.
B=percentage of total frequency of occurrence.

fruiting time for peanuts and persimmons is September and October but these fruits are available until February.

In the stomach analysis 270 different food items were recorded, but unless the items were important by themselves, they were grouped into appropriate larger taxonomic groups.

Table III lists the food present in amounts greater than one percent by volume and gives the corresponding percentage of frequency of occurrence. The percentage volume columns do not total the expected 100% because 70 items present in quantities less than one percent have been omitted from the table. These data show little variation from the gray fox diets reported from Texas by Wood (1954b) Pennsylvania by Bennett and English (1942), and Virginia by Nelson (1933). All show rabbits to be a major food comprising from one-third to one-half of the diet.

It is apparent in this study and others that certain foods are staples in the diet throughout the year. In this region, rabbits, rodents and birds represent about 50% of the annual food; 71% of the winter and 44% of the summer diet. Insects represent an important seasonal food and account for 41% of all the summer food but represent only 8% of the winter volume. Peanuts, persimmons and plums are the three main plants consumed. The former two are available from October through February and the latter only in June and July. Whether considered on a frequency or volume basis (Table III) only 18 of the 270 foods eaten represent 1% or more of the seasonal totals and only cottontails, peanuts, and persimmons in winter and cottontails and insects in summer account for 10% or more of the volume of the diet.

It, of course, does not mean that all foxes will maintain themselves on these few food items alone but it is evident that these foods comprise the main diet and any agricultural or management practice which seriously changes their abundance would have an affect on the area as a fox range.

Whether or not the food supply is a limiting factor of the fox populations in these three habitats cannot be definitely stated but the scarcity of the basic foods coincides with the scarcity of foxes and strongly suggests that fox populations are controlled by the abundance of the basic foods which are a product of the habitat.

SUMMARY

The abundance of Gray Foxes (*Urocyon cinereoargenteus*) differs greatly within local areas in the region of southern Georgia. The analysis of the contents of 171 fox stomachs in various years and places gives a suggestion of the importancs of certain basic foods. The foxes are most abundant in the areas of mixed woods and cultivation, next in areas of savannah pine and least in mixed woods with dense underbrush, and it is apparent that the abundance of foods eaten by foxes decline in this order in the three vegetation types.

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NEEDS FOR ECOLOGIC WORK IN CONTROL OF COMMUNICABLE DISEASES

Public health workers have long recognized that suppression of communicable diseases entails ecologic as well as therapeutic considerations. Although diseases that involve arthropod vectors or animal reservoirs have received more attention from ecologists than have others, modern investigations employ ecologic techniques in studies of many other preventable diseases such as cardiovascular, geriatric, and neoplastic disorders. These broader applications have interested many ecologists, but such studies have not kept pace with development in

parallel fields. Possibly because highly effective means are available for suppressing some of the prominent communicable diseases, and because the needs for ecologic approaches have not been clearly defined in study of others, deficiencies are becoming apparent as information is accumulated on many urgent disease problems. Furthermore, as objectives evolve from control to eradication, methods of suppression must become more specific and effective. These refinements usually require much greater knowledge of the natural history of diseases and often necessitate development of different bases. The purpose of this discussion is to direct attention to some of the general areas where ecologic studies are needed.

COMMUNICABLE DISEASES AND ENVIRONMENT

The relation of diseases to environment has long been recognized. Even before etiologic agents were identified, such infections as malaria and plague were associated with definite habitats; and control programs particularly against the arthropod-borne infections, have been guided by ecologic information. Control of diseases may include such diverse measures as use of therapeutic agents, vaccination, sanitation of food or water supplies, control of vectors or reservoirs, and other types of sanitation. Even the first two methods have ecologic implications, but they are not considered in the following discussion.

Ecologic information is applied to problems of disease control in several ways, *e.g.*, (1) by serving as a basis for improving effectiveness of existing techniques, (2) by indicating alternative or supplemental measures, (3) by disclosing vulnerable points in the cycles of disease transmission, and (4) by providing information on the relative importance of different means of transmission where more than one route is possible. The following examples were selected to illustrate some of the various relations of ecologic information to current problems. The concepts advanced have broad applicability, but the examples given are related to specific groups of diseases.

INSECTICIDAL RESISTANCE

Outstanding needs for ecologic studies have arisen as a result of the resistance to insecticides which some disease vectors have developed. Because certain of the "new" insecticides were so successful initially, they were used on such a wide scale that other control measures were virtually replaced in some cases. Hence the phenomenon of resistance, which is by no means new, poses a particularly serious problem at this time.

The advent of DDT and other recently developed insecticides gave early promise as effective means of controlling, and possibly eradicating, malaria and other mosquito-borne diseases. The high degree of effectiveness observed on initial programs corroborated the impression that the long-sought opportunity for practical and economical control of many diseases had been found. Increasing attention was naturally given to improvement of equipment, formulations, and regimens for application of insecticides. Consequently, work on the natural history of the various diseases, and even on bionomics of vectors against which control measures were directed, was terminated or severely curtailed.

Some of these studies have now been reactivated, as a result of the development of resistance to DDT by many arthropods of public health importance. However, investigations along this line have been much less evident than work on development of synergistic compounds to enhance the toxicity of insecticides. The latter studies are desirable, unquestionably, and obviously the most productive lines of investigations cannot be determined from available information.

In many instances, extension and acceleration of insecticidal programs have been urged on the assumption that more energetic application of chemicals can effect eradication of diseases before resistance has developed to a significant extent. Objective data to support or refute this hypothesis would be very difficult to obtain. However, survival of insects after exposure to concentrations of insecticides that formerly were lethal for the species is not due to acquisition of resistance by individuals in the population. Since resistant populations are developed as a result of selection, a more intensive selective pressure of insecticides may be expected to result in more rapid development of resistance, probably of a higher degree than would result from less intensive application. More effective means of meeting the problem of resistance may involve modification of existing techniques, substitution of other types of control, or addition of supplemental methods rather than excessive use of procedures which may magnify existing difficulties.

Paradoxically, the threat of resistance and the consequent need for ecologic studies applies with equal force to both continuing civilian-type control operations and short-term military-type operations. In the latter case, resistance may be an accomplished fact or may develop rapidly after programs begin.

Study in retrospect shows that considerable advantage would have been gained by thorough investigation of the bionomics of vectors against which such enormous quantities of insecticides would be used. "Behavioral resistance" has been attributed to some species. Many instances have been reported where changes in resting habits, dispersal proclivity, or other characteristics have resulted in insects avoiding lethal exposure to insecticides. Available evidence does not indicate clearly whether physiologic or behavioral resistance is primarily responsible for survival of insects exposed to concentrations of insecticides that were previously lethal to the species. Muirhead-Thompson (1951) has summarized and given examples of behavioral resistance to various insecticides, and Hess (1952, 1953) has abstracted more recent investigations.

There was little reason, in operation of the early programs, to consider the possibility that significant segments of the vector population might not rest on walls of human dwellings after taking blood meals, or that other alternative patterns of behavior might nullify the effectiveness of insecticide residuals when used alone. Accordingly, there have been few concerted attempts to extend information already available on the natural history of diseases against which control measures were directed.

In evaluation of control programs, many pertinent queries have been raised that are now difficult to interpret because of the uncertainty of the effect of insecticides on the initial population. For example, Renjifo and de Zulueta (1952) have pointed out that the reduction and possible eradication of *Anopheles darlingi* in some areas has been attributed to use of DDT. In a section of eastern Colombia, however, where comparable reductions occurred in populations of *A. darlingi*, concurrent decreases, as indicated by collections from stable traps, were observed in *rangeli, oswaldoi, strodei*, and *argyritarsis*. The latter species were seldom caught in human dwellings prior to the use of DDT and, hence, probably were not significantly exposed to the chemical. Explanation is further complicated by the coincident increase of *triannulatus* and *benarrochi*. Obviously, ecologic factors other than modification of the environment by DDT residual spray were affecting the mosquito fauna

during the period of observation. Adequate appraisal of this situation requires more detailed study of the species and environment.

Many conditions now exist where precontrol information is insufficient for tenable appraisal of results of control measures, and a much greater number of such situations may result from future work. It is necessary, therefore, to develop adequate background information and to establish suitable criteria for appraising control efforts. This will require much more information on the biology of vectors.

For example, several studies have indicated the possible existence of different ecotypes within the same species. Bustamante (1951) has suggested that although *A. darlingi* is a relatively domesticated species, over its total habitat range it exhibits a wide variation in extent of zoophilism. In Brazil, zoophilism is believed to be higher in the central uplands than in the coastal lowlands. The effect of DDT house spraying is consequently variable. In Venezuela and British Guiana, *A. darlingi* is being eradicated from wide areas by house spraying alone; in Brazil, however, this is not the case.

Although questions are frequently raised concerning the integrity of biologic races, *e.g.* Gillies (1945), distinct ecotypes have been recognized in some species. Control of disease vectors is directed against the specific ecotype, in some cases the entire species, that is anthropophilic. The occurrence of a subecotype in the anthropophilic segment of the species, which did not habitually rest on indoor surfaces, would not be unexpected. If competition were decreased for this subecotype by removal of the indoor-resting subecotype with insecticides, at least the relative abundance of the outdoor resting populations would be expected to increase, as was observed by Ferreira and Azambuja (1955). This factor may account for the alleged "change" in habits of populations exposed to DDT. Changes in abundance of individuals in resting places probably result when individuals that are hypersensitive to DDT are forced to seek untreated surfaces outside of houses.

More thorough evaluation of observations in ecologic context may indicate that changes in behavior of vectors do not necessarily mediate effectiveness of the control program. The objective of preventing transmission of insect-borne diseases can be accomplished with equal effectiveness by averting insects from infected individuals or by destruction of the vectors. Trapido (1952) showed that *A. albimanus* in Panama was activated to such an extent by DDT residue that many individuals did not feed. Although progressively more mosquitoes survived exposure to DDT, the irritation caused by the exposure was believed sufficient to prevent the infection of at least some of the malaria vectors. The effect of exposure over a period of eight years was the selection of a population that showed greater sensitivity to DDT as a result of destroying the individuals that were least irritated by this material. In spite of the behavioral changes, DDT reduced the number of *albimanus* feeding on humans and, consequently, has been the principal factor in reducing malaria transmission in houses treated with DDT. Conversely, before inauguration of a DDT residual spray program in the Philippines it was thought that *A. minimus flavirostris* did not rest indoors during the day. In preliminary tests, this species appeared to be irritated by DDT after a short exposure and appeared to avoid treated surfaces. A DDT-residual spray program was undertaken, however, and the subsequent reduction in malaria is attributable to the use of DDT (WHO 1956).

The fact that some disease vectors are able to enter houses treated with insecticide and obtain a blood meal without acquiring a toxic exposure does not necessarily preclude the possibility of effective use of the insecticide. Therefore, consideration should be given to the possibility of exploiting other behavior characteristics. Perhaps further information on the resting habit of the vector species may disclose resting places where vectors congregate and effective materials that are too toxic for use in dwellings can be employed safely.

Obviously, the problems associated with insecticide resistance involve many facets adaptable to ecologic approaches. The recognized limitation of insecticides should stimulate rejuvenation of interest in searches for alternative methods of control.

ARTHROPOD-BORNE VIRAL ENCEPHALITIDES

In studies of the arthropod-borne viral encephalitides, considerable information has been secured on the susceptibilty of vertebrate hosts and vectors, but precise relations in nature have not been established. Laboratory experiments on susceptibilty of mosquitoes and on infectivity of birds provide valuable suggestions of associations, but the relation of species to perpetuation of virus, *i.e.* to the natural history of the infection, requires further field studies that will provide precise quantitative data on both avian and arthropod populations. Elucidation of conditions under which these infections, usually confined to sylvan animals, are transmitted to horses and to man requires accumulation of much more environmental information.

PLAGUE

Plague is endemic in the western United States and sylvan infection persists in many species of small animals. Control of these foci depends upon acquisition of more detailed information on the epizootiology of sylvan plague. Reservoirs of plague among wild animals have long been recognized in many parts of the world and man is known to acquire infections from these sources. The relation between indigeneous sylvan infections and the devastating spread of epidemic plague associated with domestic rats is not known. The encroachment of residential and industrial developments in areas where sylvan plague is enzootic naturally causes concern over the possibility of transfer of infections from wild to domestic rodents and to man. The abortive efforts to achieve effective control of sylvan plague by controlling ground squirrels, the alleged reservoir of plague among small mammals of western United States, demonstrated that such measures were impractical. Furthermore, recent studies have shown that many of the small relatively inconspicuous native field rodents may be more important in the persistence of sylvan plague than are the ground squirrels or other larger mammals.

Investigations are now in progress to determine the extent of association of wild and domestic rodents and the degree of interchange of ectoparasites. Data accumulated by intensive trapping in adjacent habitats indicate that although domestic and wild species have specific different ecologic characteristics, a number of ectoparasites are common to both groups. Further work is needed to determine if an actual exchange of fleas takes place. If this occurs, and presumptive information indicates strongly that it may, wild rodents could provide sources of infection for domestic rats. Knowledge of the vector efficiency of fleas and the susceptibility of mammals is also essential for adequate appraisal of the potential for plague transmission. Obviously, adequate evaluation of the importance of plague in the United States and de-

velopment of preventive measures require considerably more information on the ecology of the disease.

ENTERIC DISEASES

The applicability of ecologic information to control of vector-borne diseases is more obvious than to control of infections which do not involve a sylvan host or reservoir. In many of the latter cases, however, ecologic techniques are equally useful and necessary. Many enteric diseases are attributable to improper environmental sanitation and to poor personal hygiene. The obvious answer to control is community sanitation and health education. When confronted with the necessity for effecting the maximum reduction in disease prevalence as quickly and as cheaply as possible, the relative influence of the various related factors must be determined. Ecologic studies resulting from this need have shown that certain alterable environmental factors are correlated much more frequently than others with the prevalence of some enteric pathogens, and that significant reduction in diarrheal disease can be effected with less than complete environmental sanitation, however desirable the latter may be. Further attempts to quantitate the effect of the several factors involved in perpetuation of enteric pathogens may well lead to more effective and more economical means of alleviating diseases where expensive or prolonged programs are not feasible.

Studies on enteric diseases illustrate another important principle of ecologic investigation, *i.e.* the necessity for considering diseases as entities rather than giving primary consideration to only one element of the system. Some studies have shown that *Shigella* infections can be reduced significantly by control of domestic flies (Watt and Lindsay 1948). Such methods are not universally applicable, however, since *Shigella* may be transmitted in a variety of ways. Critical studies must be made in each situation, and methods of control must be selected on the basis of specific ecologic information.

Most basic ecologic studies, such as those dealing with the broad principles of populations, have bearing on all vectors and reservoirs and on the infections for which they are responsible.

CONCLUSION

Ecology as the focal point of physical and other sciences with biologic material provides a logical field area for coordination of many disciplines that have common objectives in the control of diseases. The few foregoing examples indicate, in a general way, some of the areas where continuing ecologic work is needed. The dearth of proposals for ecologic studies has been noted by agencies sponsoring research grants, and efforts are now being made to encourage submission of projects in this area. Some of the organizations which normally support work of this type are: National Institutes of Health, Research Grants Division; Office of the Surgeon General, U. S. Army; National Science Foundation; and Atomic Energy Commission.

Cognizance must be taken of changes in direction or interest in the development of methodology for disease control, as well as in other endeavors where specific objectives can be defined in broad terms. Generally, the environment is now more favorable for work on ecologic aspects of infectious diseases than during the years immediately past.

Delineation of specific problems is beyond the scope of this discussion. Indeed, as Professor J. D. Bernal pointed out in a review of fundamental and applied aspects of research problems, finding the problem is much more difficult than finding the solution. It is not the problem, but a particular need or difficulty that stands out (Hiscocks 1956). Only a few of the needs and difficulties that require attention are indicated here.

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NOTES ON THE CARE AND REARING OF *TROPISTERNUS* IN THE LABORATORY (COLEOPTERA: HYDROPHILIDAE)*

The adults of various species of *Tropisternus* are available in numbers in almost any area of North or South America, and with proper techniques some of the species are fairly easy to rear. Several members of the genus show considerable variation over wide geographic ranges, and therefore are suitable for investigations on genetics, ecology, behavior, or evolutionary factors. The following notes on techniques for rearing may be helpful to others interested in such studies or in working out the life histories of the still unknown forms.

Containers: Adults can be kept in the laboratory for considerable periods in ordinary aquaria, but for mating or rearing work wide-mouthed individual containers are needed. Medium sized fingerbowls, pint fruit jars, or waxed containers such as those used for cottage cheese are equally good for either adults or larvae. A cover of some sort must be provided in the case of those species which fly readily. Glass squares or rounds are most useful, but covers of screen wire may also be used. The inexpensive waxed containers were used in my work because they eliminated breakage.

Wide-mouthed pint fruit jars with mason lids in which the snap top is replaced with a circlet of screen wire are useful for work in the field. Several dozen specimens were transported in such jars from Indiana to Arizona by auto and back by railway express in 1956 without loss. Pieces of aquatic vegetation were placed in each jar with three or four beetles and in the automobile the jars were kept in a box lined with glass wool sheets. A few cubes or pieces of ice placed in a jar at the center of the box kept the temperature down during the very hot periods of the day. If too many individuals are placed in a single jar, however, they may die and decompose in a very short time in hot weather.

Water: Chlorinated tap water, filtered pond water, or distilled water can be used. Raw pond water seems to increase the growth of incrusting protozoa and algae on the beetles. No great difference could be seen in the longevity or apparent health of the beetles or larvae in different kinds of water, but distilled water reduced the need for cleaning the containers. In my work the water was changed every two to four days and the containers thoroughly cleaned.

Support and Handling: Both adults and larvae apparently need some sort of support. Small pieces of vegetation (*Ludwigia*, water cress, or other) are enough. Support may be particularly important to the larvae when moulting.

Adults and larvae can be manipulated with a small strip of screen wire bent into a spoon-shaped scoop. The larvae, however, should probably be handled as little as possible. Often they can be transferred from one container to another by simply moving the vegetation to which they cling.

Food of Adults: At the beginning of my studies I assumed that the adults of *Tropisternus* were algophages, since they eat algae readily. The high mortality, however, suggested that some dietary supplement might be necessary. After some experimentation dog meal (for example Haine's Dog Meal) was found to be nearly ideal. In one experiment begun in April, 1956, eight of nine specimens of *Tropisternus mexicanus striolatus* (LeC.) fed only on mixed algae died within ten days while eight of nine fed on dog meal survived for 16 days. The survivors of this experiment, including the one survivor of the alga-fed group which was switched to dog meal on the 11th day, nearly all lived until September when after the return from Arizona they were neglected for several weeks.

Mating Behavior: Males of *Tropisternus* can be distinguished from females by the presence of a small tooth on the outer claw of the hind leg. Segregating them from the females for from three to five days usually insures that mating reactions will occur immediately when the two sexes are placed in the same container. Preliminary mating behavior was observed even between males and females of different species, but mounting and coitus was not observed except in the same species.

The details of the mating behavior have not been studied intensively, but the reactions seem to be fairly simple and similar in the three species observed. A male placed with a female after a period of segregation usually swims about at random until coming into close proximity to the female (about 1 cm). The male then orients his body toward the female, and if she swims away he follows. The female usually comes to rest after a short time and clings to the bottom or some support. If contact is made the male attaches himself to the dorsum of the female, holding on to the prothorax. If the approach was from the front or side the male quickly orients his body so that his head is toward that of the female. The male then quickly moves his body from side to side, holding on with the middle legs, and apparently touches the antennae and palpi of the female with his antennae and palpi. This may be repeated several times, after which the male moves backward, extends the aedeagus, and probes at the genitalia of the female. If the female does not move off at this point intromission may be quickly attained and coitus lasts for a few seconds up to a minute or more. After the pair separates they both usually clean the antennae and rub the hind legs together while holding to some support with the fore legs.

The preliminary following, mounting, and touching can be obtained at almost any time when segregated males and females of the same species are placed together. Copulation occurred, however, only in the spring in *T. mexicanus striolatus*, and the females may mate only once.

A more detailed study of the mating behavior of various species might produce valuable data on the mechanism of species formation. Is the mating behavior of the different species different enough to present barriers to interbreeding? How does the male recognize the female of his own species? It there an exchange of some chemical substance during the swaying-touching reaction?

Egg Laying: For life history studies, females need only be placed for a time in containers with some semi-floating vegetation. Egg cases are usually constructed overnight and can easily be found next morning attached to the vegetation. Some females will construct egg cases after a time even though they lay no eggs in them which may indicate that they have not mated. For any genetic work, teneral (= callow) females should be sought in the field and held until ready for mating.

Care and Feeding of Larvae: The eggs hatch in two or three days and the larvae emerge from the case. The

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egg cases must be watched closely so that the predatory larvae can be segregated immediately after hatching or only a few will survive the first day.

The first-instar larvae can be fed a few hours after hatching by presenting small larvae of other insects with forceps. They will usually grasp anything which moves close to them. Hand feeding is most effective in getting rapid growth because larvae will go for some days without catching live food merely placed in the container with them.

Drosophila larvae, raised in small tubes with agar, and wild-caught and reared anopheline and culicine mosquito larvae were used in my rearings. Food was offered several times a day and the larvae seldom refused it. Pipetting the mosquito larvae onto filter paper greatly speeded up feeding since they could be grasped quickly with the forceps. As the *Tropisternus* larvae grow their appetite increases and larger insects (odonate naiads, etc.) can be fed. Second and third instar larvae will also accept pieces of hamburger or horsemeat, but this necessitates more frequent cleaning of the containers.

Pupation: When the larger third-instar larvae begin to refuse food, the containers should be prepared for pupation. With the pint waxed containers this is easily done by pouring in dry sand until a slanting surface is formed from one side to near the top. Only a little water need be left in the container at this time, but the level should be kept constant to provide a stable gradient of moisture in the sand. The sand should be of intermediate or fine texture; coarse sand seemed to be unsuitable for forming the pupal chamber.

The containers should be covered at this time if not previously because the larvae soon leave the water and may escape completely if not restrained. Usually they burrow into the sand, but the pupal chamber may not be formed immediately. When formed the chamber is usually about an inch above the water level where the sand is moist, but will not slump. After it is formed the sand may dry considerably without the chamber collapsing so that some material from the larva may be incorporated into the walls. In several cases, I opened the chamber by slicing away the sand with a scalpel, and then closed it again with a piece of cellophane in order to observe the larve and pupa within.

The highest mortality in the larval stages is during the first few hours after hatching and during the period after the third-instar larvae quit feeding. The long prepupal stage may be due to a natural diapause or failure to provide suitable conditions for constructing the pupal chamber.

Duration of Stages: The following Table I summarizes rearings made at Bloomington, Indiana, and at the Southwestern Research Station of the American Museum of Natural History in Arizona. The numbers in parentheses indicate the survivors at each stage on which the range of dates is based, but do not indicate natural mortality since specimens were preserved for life-history studies from time to time:

Conclusions: The rearing procedure outlined may sound complicated, but it can actually be carried out with a minimum of attention. The feeding and care of the larvae of *T. lateralis nimbatus* at Bloomington was largely done by my nine-year-old daughter who came to the laboratory for a few minutes each morning. The care of over forty containers of beetles and larvae in Arizona seldom took more than an hour each day. It seems, therefore, that the species of *Tropisternus* may be suitable for a variety of kinds of biological investigations. They are not as suitable for genetic work as insects with a shorter life cycle, but there are other advantages associated with the ease with which the adults can be collected and studied.

TABLE I. Duration of stages in various species of *Tropisternus* reared in Arizona (SWRS) and Indiana (Ind.) during 1956

Species and place of collection and rearing	*Tropisternus natator* D'Orch. Oklahoma (SWRS)	*T. lateralis nimbatus* (Say) Indiana (Ind.)	*T. lateralis subsp?* New Mexico (SWRS)	*T. mexicanus striolatus* (LeC.) Indiana (SWRS)
Female collected	vi.13	iv.8	vii.3	v.6
Egg case deposited	vi.18 (1)	iv.28-30 (1)	vii.8-10 (1)	vii.9-10 (1)
Hatching	vi.22 (20)	v.2-5 (10)	vii.13 (5)	vii.13 (18)
First moult	vii.2-3 (3)	v.7 (4)	vii.19-24 (3)	vii.16-20 (13)
Second moult	vii.7-9 (3)	v.10 (3)	vii.21-27 (2)	vii.21-27 (12)
Larvae left water	vii.20 (2)	.....	viii.8 (1)	viii.1-8 (8)
Pupa formed	viii.1-2 (1)	v.30 (1)	viii.10 (1)	viii.10 (1)
Adult emerged	. .	vi.5 (1)	. . . .	. . .
Days from egg to pupa	44	32	31	32

SUMMARY

Adults and larvae of several species of water beetles of the genus *Tropisternus* can be maintained under laboratory conditions and reared. Adults feed readily and live for long periods on commercial dog meals. Larvae can be reared in wide-mouthed containers with almost any kind of water. Hand feeding with larvae of other small insects seems to give the best over-all growth. Sand slants giving a stable moisture gradient are necessary for pupation. Rearing from eggs to pupae takes from 32 to 44 days depending upon the species involved. The numerous species of this genus offer many opportunities for laboratory studies of ecological, behavioral, and evolutionary problems.

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A POSITIVE CORRELATION BETWEEN RELATIVE HUMIDITY AND THE DISTRIBUTION AND ABUNDANCE OF *AEDES VEXANS*[1]

A positive correlation has been demonstrated between relative humidity and the distribution and abundance of the mosquito, *Aedes vexans* Meigen.

The field installation at which the observations were made (Platt 1957) consists basically of two fifty-foot wooden towers located in the ecological extremes of an open field and dense woodland, each tower being equipped with instruments for automatic recording of microenvironmental gradients. Aminco-Dunmore type electric humidity and temperature indicators have been placed at

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the O, 3, 6, 15 and 50 foot levels, each complete set being fed into a 16-point strip recorder. The humidity indicators cover the relative humidity range from 6-99% at 80° F with a declared accuracy within ±1.5% R. H. These sensing elements are in continuous equilibrium since their speed of response of 65% of total change within twelve seconds is faster than changes which occur naturally. The almost simultaneous recording of temperature and relative humidity makes possible the calculation of absolute humidity and vapor pressure. Recording anemometers are at the 3 and 50 foot levels, and recording rain and surface water level gauges are near the base of each tower. Portable instruments provide for supplementary environmental data on radiation, light, wind, temperature and humidity.

All the mosquitoes used in these correlations were obtained from a special series of light trap collections. The traps were arranged in two batteries of twelve traps each, with a separate battery on each tower. The twelve traps were operated consecutively for one hour periods each through the night from 6:00 PM to 6:00AM. The batteries were operated one night per week sequentially at 6, 15 and 40 foot elevations.

Of the more than twenty species of mosquitoes caught in these traps during the experimental periods, only one species was obtained in sufficient numbers to provide adequate data for correlation analyses. This paucity resulted from severe droughts of the past three years which have severely, though temporarily, reduced mosquito populations.

For the 18 month period from January, 1956, through June, 1957, only 17 collections were adequate for analysis. In the majority of unused collections, the catch was too small, with less than five mosquitoes being caught for any one hour, and in many cases less than that for the entire night. For other unused collections, in which the catch was adequate, the relative humidity was above 90% for all or most of the night (*cf.* first graph in Fig. 1) thus denying the mosquitoes an opportunity to make a choice in a favorable range. A few were not used because of high winds or mechanical failure. The 17 collections which have been analyzed were about evenly divided between the woods and field, and between the elevations of 6, 15 and 40 feet. They were also scattered through the spring, summer and fall months.

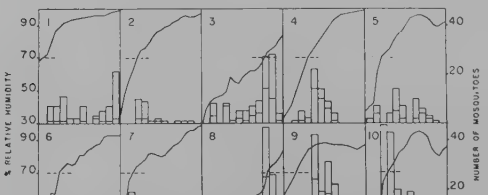

FIG. 1. These ten graphs each represent the mosquito catch for a night, the bars in each graph representing successive hourly catches. The dotted lines on the relative humidity curves mark the 70% level. The first graph is illustrative of the lack of positive correlation when the humidity is 90% or above for most or all of the night; the other nine being illustrative of positive correlations. Graphs 1, 2, 6 and 8 represent 6 feet; 3 and 8, 15 feet; and 4, 5, 9 and 10, 40 feet. Nos. 2, 8 and 10 represent the woods, and the others the field.

For every one of these 17 usable collections, a positive correlation was obtained between relative humidity and the maximum catch through the night. This correlation was noted by plotting relative humidity with the mosquito catch. Numbers of mosquitoes caught increased with relative humidity until an "optimum" was reached, but the numbers decreased with further increase in relative humidity. Relative humidity values for the 40 foot level were interpolated from the 15 and 50 foot observations.

Graphs for the first nine of these 17 nights are presented in Figure 1 (Nos. 2-10 inclusive). Data for the other nights were not obtained until after Figure 1 was prepared, and as these data were similar to that presented in Figure 1 another figure did not seem necessary. The graphs have been arranged so that the ones on the left (Nos. 2, 6, 7) were obtained at the six-foot level, the two in the middle (Nos. 3, 8) at the 25-foot level and those on the right (Nos. 4, 5, 9, 10) at the 40-foot level, and are about evenly divided between the woods and field. For eight of these 17 (illustrated by Nos. 2, 3, 4, 7, 8, 10) the maximum collection is at 70% R. H., and for the other nine (illustrated by Nos. 5, 6, 9) the maximum catch was obtained between 60 and 90% R. H.

These relative humidity correlations were the result of a systematic search for possible correlations, singly and in all combinations, of the distribution and abundance of *Aedes vexans* with each of the environmental variables recorded. The only positive correlation obtained was with relative humidity. Included among those factors showing no correlation were: absolute humidity, temperature, a combination of absolute humidity and temperature, and a combination of relative humidity and temperature.

In an effort to evaluate the observed correlation between humidity and mosquito activity, similar analyses were made of data obtained on 73 nights during which collections were made for three hour rather than one hour intervals. These data demonstrate a generalized pattern of much larger numbers for most species being collected in the earlier rather than the later parts of the night (Love, Platt and Goodwin, unpublished). Since humidity increases through the night, and usually goes above 90% before morning, relative humidity may be the primary factor responsible for this distributional pattern. However, no precise correlations could be obtained with these three-hour collection periods, thus indicating that the frequency of collections must be at least of the order of hourly ones, as used in this paper. Shorter intervals may give even clearer results.

Although no experimental work on reactions of *Aedes vexans* to atmospheric moisture has been found, several excellent studies exist for other species. The more critical laboratory studies on effects of humidity have been those in which gradients were utilized. In experiments with *Anopheles maculipennis* and *Aedes aegypti*, Martini and Teubner (1933) found that both species showed a general preference for higher humidities, although this reaction was not always sharp. A pattern consisting of high humidity preference up to a point, indifference, and then low humidity preference was reported by Rudolfs (1923, 1925) for *Aedes sollicitans, A. cantator*, and *Culex pipiens*, and by Thomson (1938) for *Culex fatigans*. Differences indicated for optimum humidities evidently depended partly upon the species involved. In studies using an olfactometer, Brown, Sarkaria and Thompson (1951) found that moist air at 85% R. H. attracted three to five times as many *Aedes aegypti* as dry air at 15% R. H. Brown (1951) found in field studies with Aedes mos-

quitoes that above 15° C moisture was the chief attractant factor.

Perhaps the most detailed series of humidity experiments carried out to date have been those of Platt, Collins and Witherspoon (1957) on a laboratory strain of *Anopheles quadrimaculatus*. Their experimental population variability was quite high, but for most of the individuals tested, the optimum relative humidity was found to be between 70 and 80%, there being a sharp avoidance of higher as well as of much lower humidities. These reactions were temperature independent over the range of 15 to 30° C and were also independent of light intensity and color.

In conclusion, a 100% positive correlation has been demonstrated in nature between relative humidity and the abundance of *Aedes vexans* through the night, regardless of elevation, time of night, or habitat (woods or field). The optimum humidity for eight of the 17 nights observed was 70%, and for others between 60 and 90% R. H. This wide humidity spread of 60 to 90% may be accounted for by a possible high species variability coupled with relatively small collection numbers as the result of continued droughts in the area.

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QALI, A TAIGA SNOW FORMATION OF ECOLOGICAL IMPORTANCE

The effects of snow as an ecological factor have received very little attention in the English-language biological literature. Indeed, English itself, having evolved in a temperate maritime climate, is extremely poor in terms for various snow phenomena. Monolingual biologists studying the vertebrates of the taiga and tundra are immediately at a disadvantage by not having readily available a concise terminology for describing and discussing snow conditions and the reactions of animals to them. Formosov (1946) in his classic work on snow as an environmental factor gave a number of precise snow terms taken from the languages of various northern European and Siberian peoples. This aspect of the work is not mentioned in the abstract given in the Arctic Bibliography (vol. 4, entry no. 21870, p. 302). English-speaking biologists should be advised that there exists a rich source of concise terms for various snow phenomena in the languages of not only northern Eurasia but of northern North America as well. Since snow is undoubtedly one of the most important factors in the ecology of northern vertebrates, these terms should be adopted into the English-language ecological lexicon.

Both the Athabaskan and Kobuk Valley (forest) Eskimo languages of Alaska, as well as the unspecified Siberian languages given by Formosov, have precise terms for the snow that collects on trees. The Athabaskans of the Fort Yukon region, Alaska, use the term *žá* for "snow" in a general sense and *dé-ža* for "snow that collects on trees." The Kobuk Valley Eskimo, in addition to the word *anniu* for "snow" in a general sense, have the words *api* for "snow on the ground" and *qali* for "snow on the trees."

The phenomenon of qali[1] and its importance are not well understood by biologists of the temperate zone, since it is dependent on (1) lack of wind in the winter, (2) very low quantities of incoming solar radiation and (3) continuously low ambient air temperatures. These conditions are fulfilled during the almost windless winter in interior Alaska, where the snow accumulates on all exposed non-vertical surfaces with little loss from sublimation. Formosov recognized its ecological importance by noting (*op. cit.*) how the arboreal activity of marten (*Martes martes* L.) was influenced by it. I have also noted (Pruitt and C. V. Lucier, unpublished data) that the winter activity of red squirrels in the taiga of interior Alaska is influenced by this phenomenon, as well as by temperature (Pruitt and Lucier, in press). There is also some evidence that chickadees (*Parus atricapillus* and *P. hudsonicus*) in the Fairbanks region exhibit vertical migrations, upwards to the birch and aspen covered hills where the more frequent winds keep the trees "cleaner" and back down into the valleys whenever the trees there are free from qali.

During the observations on red squirrel activity it was soon apparent that some objective measurement of qali formation and fall would have to be made, since written descriptions were too long and involved and were too

[1] *Editor's note:* the consonant *q* without *u* is rare in English, but occurs in numerous place names transliterated from Arabic as well as from Eskimo. It is the linguist's symbol for a postvelar stop, more guttural than *k*. English-speaking users of the new name are at liberty to pronounce it "kali" except when speaking Eskimo.

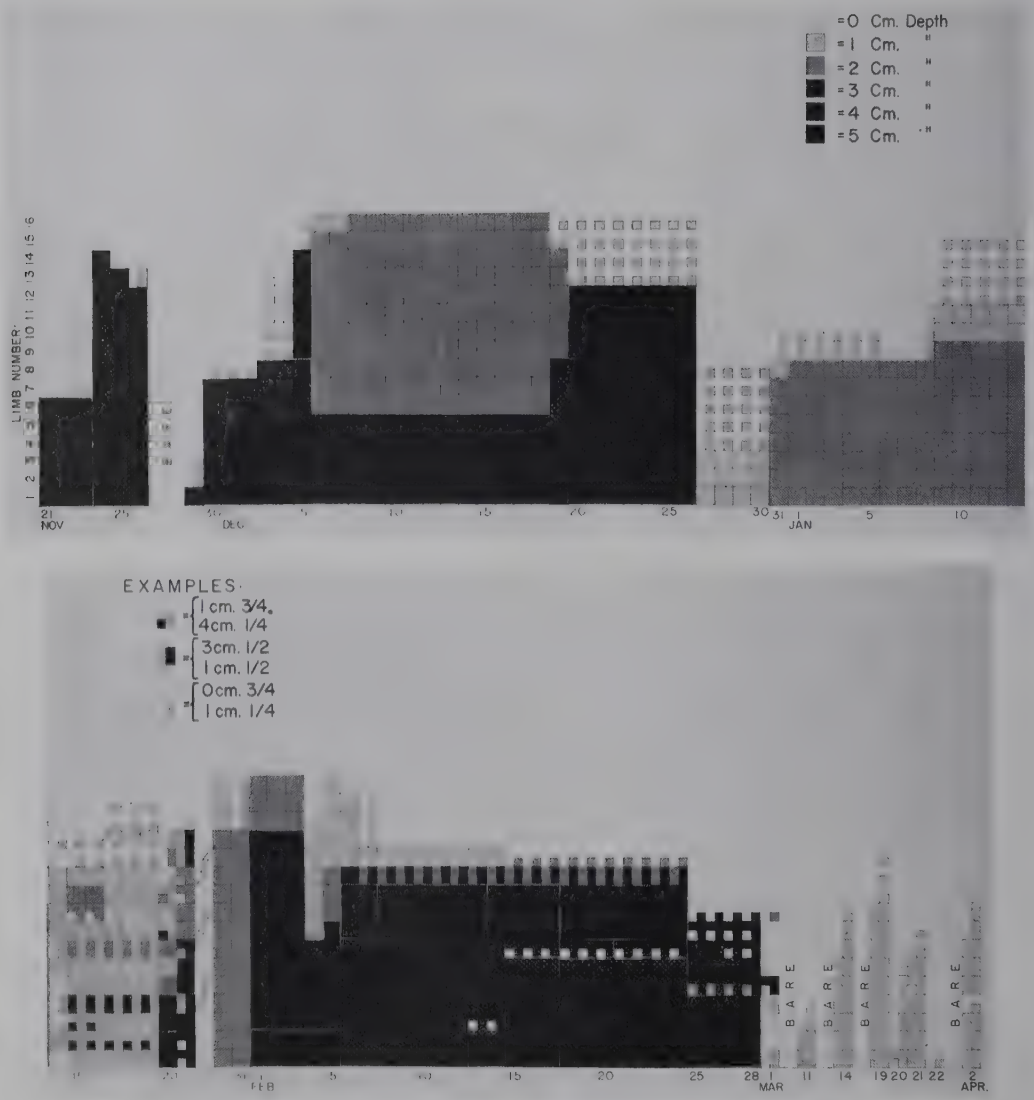

FIG. 1. Diagrammatic representation of qali accumulation and fall, winter 1956-57.

subjective. Therefore I have attempted to standardize these observations by correlating qali formation in the spruce forest with qali formation on a set of standardized "artificial limbs" or a "qalimeter."

Ordinary birch dowels may be obtained in 1/16 inch gradations from 3/16 to one inch at most lumber yards. Search revealed 1/16 inch and 1/8 inch sizes at a model airplane and hobby shop. These 16 dowels were fixed to a frame at approximately four-inch intervals so that they projected horizontally at right angles to the frame for about 18 inches. They were arbitrarily numbered from one through 16, from the thickest to the thinnest.

This qalimeter was set up on a bioclimate study plot in virgin white spruce forest (Pruitt, in press) where it could be observed while making the other periodic bioclimatic observations. Although it was installed after the winter snow had started to form, readings were not begun until after a wind had removed the small amount of qali already accumulated. Therefore the qali on the device had the chance to build up and fluctuate the same as did the qali on the trees.

Figure 1 is a graphic representation of qali accumulation and fluctuation as recorded by the qalimeter during the winter 1956-57. Since the primary purpose of the qalimeter is to furnish an objective measure of the state of the qali instead of being forced to use complex sub-

jective verbal descriptions, the following extracts from field notes should be compared with Figure 1 to indicate the agreement of qalimeter readings with natural conditions. Note that the observations were interrupted for a short while in January.

The snowfall during the period 21-24 November 1956 built up the qali from zero to almost complete. Light to gentle northeast winds during 26-27 November resulted in a reduction of qali to zero. 26 Nov.—"Some qali fall, snow surface littered with needles and cratered." 27 Nov.—"*No* qali on trees, completely bare; snow very compact, surface littered with needles about one per four cm^2; also many poplar and alder leaves." 29 Nov.—"Trace or dust of qali on trees." 30 Nov.—"Slight qali buildup." 6 Dec.—"Very fluffy qali accumulations over week-end, even tiny twigs covered, very unstable." The snowfall that occurred the first few days of January (1957) did not cause qali cover to form on bare twigs, but only increased that already formed. 14 Jan.—"Qali forming, many craters on snow surface, several spruces bending." The heavy snowfalls during 12-21 January caused qali formation described as "compact, not falling easily; twigs of Larix and dead trees bare. . . ." ". . . large complex flakes falling, forming qali increments rapidly, hanging on to any surface they touch. . . ." ". . . much qali fall and accumulation, many trees leaning." 6 Feb.—"Full qali, except for tiny twigs, many new leaning trees." 7 Feb.—"Some qali and craters." 14-18 Feb. —Light to moderate north and west winds. "Swaying spruce tops, few flecks of qali fall . . . some qali fall and cratering but remarkably little considering the wind force. . . . Craters, many broken branchlets on snow surface. . . ."

The thaw of late February and early March cleaned off all qali except a few large chunks on leaning trees and broken tops. Most of the fall occurred on 28 February-1 March and was described at 1105 28 February as "Much qali fall, constant crashing and crackling. Tips of spruces bare. Sky clearing as I stand here and about 15 minutes sunlight on a qali chunk causes it to fall." On 1 March at 1115 the forest was described as "Most of qali gone, forest has open aspect. . . . Api surface pitted and cratered. Fallen qali has caused a crust to form, but only under trees, not in forest openings where api surface not pitted."

A light snow on 10-11 March caused a dusting of qali to form only on needle-bearing branchlets and large bare branches. 19 March—"Heavy wet snow; forming qali on all but small twigs. Qali = 1 cm., .9 cover." 2 April —"Dusting of qali."

Thus a qalimeter of this simple construction provides an objective method of describing and recording the amount and method of accumulation and fall of qali—the snow that collects on trees. It permits standardized observations to be made comparing qali accumulation and fall between different winters and different places.

Three years of almost daily observations on this plot of virgin spruce forest near Fairbanks have resulted in the accumulation of numerous observations of the effects of qali on both animals and plants. See Pruitt (*op. cit.*) for a more complete description of the plot and its climates. When this study was first begun several groups of spruces broken off in a characteristic fashion were noted on and near the plot. Seventy-seven per cent of the breaks on the plot were between 13 and 30 feet above the forest floor and the broken tops within each group were usually oriented in the same direction. On this one-acre plot 94 trees of all sizes have been broken by qali accumulation. At first it was believed that these were the results of wind-throw. During the winter 1955-56 one such group was observed to enlarge because of breakage due to qali accumulation. During the winter 1956-57 another group was seen to develop due to qali breakage. These groups give all the appearances of typical wind-throws and are incipient glades. They would undoubtedly be interpreted as wind-throws by an observer familiar with the forest in its snowless condition only. Their true origin becomes apparent only upon repeated observations throughout the year. Because of the frequency of these and similar observations I conceive of qali being a major factor controlling one of the "climax" vegetational complexes of the region. Many years of daily observations and measurements on protected areas of spruce forest will be necessary to confirm these ideas. Unfortunately, no accessible protected areas of typical interior Alaska spruce taiga have even been established as yet.

According to my concept, the succession is as follows: White spruce grows to a pole-stage or larger. Qali formation causes breakage in a small area of two or a half-dozen trees. This opens the canopy and causes the formation of a glade or "forest window" (Formosov). The young trees adjacent to the glade respond to the increased light by increasing growth on that side, thus shifting their mass from more or less equal distribution around the vertical axis to more on the side toward the glade. This causes them to be even more susceptible to breakage by qali formation in future years, for once a spruce departs from the vertical position it is almost surely doomed to qali breakage. The glade grows until some optimal size is reached. The factors causing the growth to stop are probably (1) size large enough so that wind circulation prevents qali buildup and (2) canopy opening large enough so that the minimal solar radiation prevents qali buildup (Geiger 1950: 349-356). Other factors undoubtedly are operating here. Because sunlight can now reach the forest floor and because competition with the spruce is reduced, the glade is invaded by herbaceous plants, to the gradual exclusion of the typical sub-spruce carpet of mosses. The heavy rain of needles from the drying broken spruce tops aids in smothering the mosses. These are followed by willow, alder, birch and aspen. These deciduous shrubs and trees grow and mature, resulting in a forest floor of decaying leaf litter instead of the solid carpet of mosses. In this leaf litter white spruce can ecise, which it cannot do in the thick carpet of mosses under a mature stand. Thus the resulting vegetation is a mosaic of even-aged stands of white spruce interspersed with blocks of various-aged stands of willows, alders, birches and aspens. Qali breakage of only scattered single trees in the white spruce forest acts to release the neighboring trees from competition. This explains the great disparity in size of trees in even-aged stands.

The "climax" then, is not a self-perpetuating vegetational association as the classic concept would have it, but a dynamic cycle of white spruce-glade-deciduous trees-white spruce. I use the term "climax" to refer to the stable floodplain white spruce mixed forest or Phase II in the terminology of Drury (1956). Drury is undoubtedly correct in questioning the use of the term "climax" at all when referring to the vegetation of the North. Possibly the simple term "stable vegetation" would be better, since it has no successional or organismic implications.

This concept of one of the types of stable vegetation of interior Alaska explains several anomalies which have been noted in the vegetation of the region. First it explains the occurrence of even-aged stands of white

spruce which consist of trees of greatly different sizes. It takes into account the observation that white spruce appears to be unable to reproduce itself under its own cover. It explains the mosaic pattern of the taiga vegetation.

ACKNOWLEDGMENTS

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SUMMARY

1. Because of the paucity of English-language terms for snow conditions, biologists studying the vertebrates of the north are urged to draw upon the rich source of snow terms found in the languages of the peoples of northern Eurasia and North America.

2. The ecological importance of one taiga snow formation (*qali*—the snow that collects on trees) and its role in controlling one of the vegetational associations of interior Alaska are discussed.

3. A method for standardizing qali observations is described.

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OCCURRENCE OF *LIMNORIA TRIPUNCTATA* AT THE CAPE COD PENINSULA

e research on which this observation was based was aided by a contract between the biology branch of the Office of Naval Research, NONR 266(41) and the Lamont Geological Observatory of Columbia University. L.G.O. Contribution No. 273, Biology No. 20.

Prior to the monograph by Menzies (1957), there had been no verified records of *Limnoria tripunctata* Menzies north of Providence, Rhode Island.

Menzies (1957) recorded one specimen collected from Boston by the William F. Clapp Laboratories. This record might be subject to question because the majority of specimens collected from Boston consisted of *Limnoria lignorum* (Rathke). On July 6, 1957, Miss Carolyn Beckman collected a large sample of *L. tripunctata* from a locality north of Woods Hole, Mass., between East Falmouth and South Mashpee. This establishes beyond doubt the occurrence of the species in the Cape Cod region.

This is a matter of some economic importance because of the ability of the species to penetrate creosoted wood. It is a matter of academic importance because this locality probably represents what must be close to the northernmost limits of the range of this species. It is probable that the species occurs at Woods Hole. It has not, to our knowledge, been reported in any faunal list from that locality.

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COMMENTS ON THE BLACK AND SQUARE-LIPPED RHINOCEROS SPECIES IN AFRICA

During the latter part of July, 1957, my wife and I were fortunate enough to be able to spend a short time at the two reserves in Zululand, Hluhuwe and Umfolozi, which are still the home of the Black Rhinoceros, *Diceros bicornis bicornis* and the Square-lipped (formerly called White) Rhinoceros, *Diceros* (*Ceratotherium*) *simus simus*. I was most interested in assembling any observations on the behavior of these species which might supplement previous observations made on the Great Indian Rhinoceros, *R. unicornis* (Ripley 1952) or comments on the population structure made by Hutchinson and Ripley (1954). During our stay we were given every assistance and aid by Mr. C. J. Ward, resident ecologist for the Natal Parks, Game and Fish Preservation Board in Zululand. Mr. Ward has made many interesting observations and it is to be hoped that he will publish them in the future. Meanwhile, he is making an important study of the food preferences of these two species, which as Attwell (1948) has pointed out are not in competition, the Black being a browser, feeding on the tips of the branches of euphorbias, *Acacia*, and *Spirostachys* species, while the Square-lipped grazes on grasses and small shrubs.

The Hluhluwe and Umfolozi Reserves are situated about twelve miles apart, some twenty miles inland from the coastal highway of Natal not far from the small towns of Mtubatuba and Hluhluwe. Both reserves are somewhat small, nearly fifteen thousand, and somewhat over thirty thousand acres respectively, and it is to be hoped that additional lands adjoining them can be secured in

order to prevent overcrowding of the resident game, a considerable potential problem in view of the lack of predators.

Shortridge (1934) quotes a 1929 estimate of 120-150 Square-lipped Rhinos in the Umfolozi Reserve, whereas current estimates are in the neighborhood of 500 animals. There is thus a serious potential conservation problem for the authorities in the large-scale increase in numbers of this rare species on its restricted range.

The Black Rhinoceros, which is more common in the smaller reserve of Hluhluwe, probably now numbers over 200 individuals.

BREEDING

Evidence is somewhat circumstantial, but both Black and Square-lipped Rhinos appear to mate in the Zululand Reserves at almost any time of year. Mr. Ward reports that calves appear approximately twice a year as "winter calves" or "summer calves." We observed a very small Square-lipped calf, perhaps two weeks old, on July 26, and two calves on the same day, aged between one and two months. The Black rhino has bred in captivity recently at the Rio de Janeiro Zoo, Brazil, where we observed two young in May, 1956, one aged two months, the other two years. The Director, Mr. Baretto, told us that the pair were placed together when secretion from the female was noticed, and that coupling went on for nearly the full term, or seventeen months. The cow carried her calves for eighteen months in each case. The bull was very aggressive and had to be separated from the cow before the birth of the young. In addition to these records at Rio de Janeiro, the Black Rhino has bred in captivity at Chicago, Illinois, and, in 1957, a calf was born at Frankfurt, Germany. Recently, an Indian Rhino calf was born at Basel, Switzerland, in September, 1956. (Lang 1957.)

TERRITORY

In my discussion of the Indian Rhinoceros (1952) I suggested that these animals maintain a territory during part of the year. That such a territory is capable of compression, and may indeed fluctuate, and that the aggressive behavior of the animals themselves may alter with the seasons has been indicated by Gee (1953a, b). It does seem appropriate, however, to assume from the evidence that the Indian rhinoceros holds a territory during part of the year, which does not appear to be a breeding station.

In the case of the Black Rhinoceros, such evidence as exists points to the assumption of a territory which is defended by the male, and in which the female and young may also occur. The Black Rhinoceros seems more sociable in this sense than the Indian species, although solitary animals also are seen commonly. Individuals of this species have a notoriously uncertain temper.

Mr. Ward showed us an area in the Hluhluwe Reserve which he said had formerly been occupied by a rather small old bull, a cow, and a calf, the territory centering around a small pool or pan. He had become accustomed over a period of several months to seeing this family in this area, which appeared to be their home range. On one occasion while watching the cow and calf at the pan, Mr. Ward had seen a large, strange bull approach. In appearance he noted at once that this bull seemed, as he put it, "uncertain." After a short time, the smaller, old bull came into view, and the stranger either saw him or caught his scent. The large stranger at once turned and made off rapidly. The old bull did not notice this, but came up to the pan, rubbed noses with the cow, then appeared to patrol the area deliberately scenting. At the point where the stranger had made off he appeared to catch the scent of the intruder, for he immediately turned and followed at a trot, apparently in pursuit. Mr. Ward was unable to see whether the two bulls encountered each other. This territory then may be a beeding station for the male, or indeed it may be a home range for this pair with young. The evidence seems inconclusive on this point.

The Square-lipped Rhinoceros has a far greater threshold of tolerance for individuals of the same species. We commonly saw groups ranging from a pair to four animals together, and five or six at one time have been seen commonly, although there is no evidence that larger groups may not simply have made a temporary aggregation in a favorable feeding area.

On one occasion we observed what appeared to be a family party consisting of a bull and large cow Square-lipped Rhino accompanied by a smaller cow. Our impression, in which Mr. Ward concurred, was that the second cow was a daughter. It appeared from its size, the size of the horn and the condition of the skin to be a young animal. In addition to this trio, who seemed completely at ease and representing a family unit, there was a young bull of perhaps four to five years in attendance. This animal was not allowed to graze closer than about 100 yards from the trio, at which point it would be chased with a short rush or series of snorts and a shooing motion of the head by the bull principally, aided to a lesser extent by the two cows. No physical violence accompanied these demonstrations. The young bull never turned and disputed the ground. Without being certain, of course, it appeared to us that the younger bull was a grown-up calf being encouraged to leave the family. The threshold between tolerance or playfulness and antagonism seemed to be too low to permit an assumption that the younger bull was a stranger or a challenger. Beyond this, we could make no concrete estimate of territory in the Square-lipped Rhino. Mr. Ward reported that he was accustomed to seeing certain family parties including recognizable individuals, known by the size or shape of the horn, in certain areas for periods of time. However, some sort of color banding or marking would be needed to be able to trace the movements of individuals accurately.

DUNG HEAPS

Both the Square-lipped and the Black Rhino defecate in special places thereby making heaps of dung. These dung heaps can be readily distinguished as to species as Shortridge (1934, *tom. cit.*) and others have noted, as the diet of the two species affects the character of the dung itself. The dung heap is in general rather similar to that of the Indian Rhino, near a trail, and often, in the case of the Square-lipped, of similar dimensions, a conical heap several feet in height. The dung heap of the Black Rhino is always smaller and more scattered. In both species there is usually a depression in the ground to one side, or near the center of the heap. The defecating animal places its back legs in this depression and often stretches and kicks out with its legs alternately as it defecates, rather as a dog does. This depression then seems to be partly created by the animals, the ground perhaps being softened by their urinating at the same time. However, I believe it is often created secondarily by the visits of birds such as francolins and guinea fowl, mongoose, and large lizards, *Varanus* sp., all of which dig in the ground for seeds and beetle

larvae. With regard to the Black Rhino it seems that these spots as well as the habit of urinating along the trails are methods of marking a territory. I am inclined to think such a territory represents both a breeding station and a home range. Rubbing sticks, which are frequent, presumably serve the same purpose and additionally may carry the scent of the secretion of the characteristic sores which the Black Rhinos possess on the anterior median portion of the flanks, just posterior to the heavy shoulder fold. These sores have been described, although the physiology of the condition is not understood, by Attwell (1948, *tom. cit.*) and others.

In the case of the Square-lipped Rhino, the dung may serve to identify the presence of individual animals, although there is only the vaguest evidence that the species has anything more than a broadly-defined home range. Rubbing sticks, often tree trunks, are also used in this species, but sores are not noted. Mr. Ward feels that in the Square-lipped species, but not in the Black, the dung heaps may be visited by several individuals for the following reasons:

(1) An animal comes upon a dung heap and by association, decides to utilize it.

(2) Dung heaps are often on ridges. Their use comes then after a long hard climb when the exercise makes the animal feel like using it.

(3) Some sort of traditional spot for a resident animal to defecate at.

There is thus an indication that a dung heap in the Square-lipped species may serve as a sort of family bulletin board, chronicling the news of the whereabouts of the group. In a more loosely-knit way, it may also serve as a territorial marker.

SUMMARY

A discussion of the Zululand Reserves, last home in southern Africa of the Black Rhinoceros, *Diceros bicornis*, and the Square-lipped (formerly White) species, *D. simus simus*, gives some idea of the numbers and status of these species. Evidence of the breeding cycle and the possession of territory is given, especially in the light of a previous study of the Great Indian Rhinoceros, *Rhinoceros unicornis*. In these species, as in the Indian one, considerable importance is given to the creation of dung heaps, used presumably as some sort of territorial marker.

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REVIEWS

The Pleistocene Environment[1]

Soon after its publication ten years ago Glacial Geology and the Pleistocene Epoch won for itself a remarkable position in geological literature. It was the source to which research workers turned for a comprehensive critical summary of the Ice Age. It was also a lucid and stimulating textbook that fired the imagination of many students beginning their study of the latest and fullest chapter of the earth's history. Its frequent citation in the bibliography of papers dealing with biogeography and paleoecology shows how often it has provided a painless introduction to glacial geology for biologists.

Many old friends will welcome the appearance of Professor Flint's new book on the same subject. The past ten years have seen a great increase in knowledge of the Pleistocene. The application of isotope geochemistry alone would have sufficed to render the early summary obsolete; but there have been other important advances as well—the establishment of a deep-sea stratigraphy, drift mapping in remote parts of the world, pollen analysis of interglacial deposits, especially in Europe, and the intensive study of frozen-ground phenomena.

Many second editions of successful textbooks are but slight variations on the original theme. The present work is a refreshing exception. It is, as the title implies, not a revision but a complete new book. The plan of organization is similar to the old one, and ten years' accumulation of new evidence has not noticeably modified the author's views on hypotheses of the origin of glaciers; but almost all of the text, the maps, the line drawings, and the photographic illustrations are new.

More important, there has been a major shift in emphasis. Though it differed from most geology texts in its concern with process, the early book was essentially descriptive. Long chapters were devoted to cataloguing the glaciers and past glaciation of the surface of the earth, and to the stages in the history of the Great Lakes. In the present text this material has been cut to a bare minimum and its place taken by a longer discussion of glacier regimen and meteorology. This emphasis on process is present throughout the book. There is an obvious attempt to tell not only what happened but to explain how the system worked.

In addition, there are full chapters on frozen-ground phenomena and deep-sea stratigraphy, subjects that received only passing mention before. Radiocarbon dating and oxygen thermometry fit into the previous system of chapters but revolutionize the treatment of chronology and temperature.

In treating these new subjects Flint moves with a sure step. There is no fumbling, none of the half-truths that betray the author who is beyond his depth. In a few instances, however, apparently contradictory hypotheses are presented with the comment that there may be truth in both. Fuller explanation of the circumstances under which each hypothesis might be valid would be helpful.

For biologists the summaries of plant and animal fossil evidence, including tables prepared by specialists in Pleistocene paleontology, are of particular interest, but no part of the book has more biological significance than the discussion of equatorial deep-sea cores. It appears from oxygen thermometric measurements on the shells of pelagic foraminifera from the deep Atlantic ooze that the equatorial mean annual surface temperatures have undergone changes of about 6°C between glacial and interglacial periods. It is clear that glacial cooling occurred throughout the world and was not restricted to the middle and high latitudes. This has direct bearing on some widely-held views about the nature of the extra-glacial biota during ice ages. For example, it cannot be reconciled easily with the idea that the forests of the southern Appalachians have not changed since early Cenozoic times. To the reviewer it suggests that the biota of tropical regions, particularly of tropical oceans, must be out of harmony with present conditions. Presumably the species unable to tolerate mean temperatures 6°C lower than current ones were extinguished at the end of the Pliocene, and any ecological replacements evolved during interglacial times must have been obliterated by succeeding glaciations. The present day tropical biota ought to display evolutionary drift toward adjustment to present high temperatures.

Although it summarizes a great deal of information useful to ecologists the book is written primarily from a glacial geological point of view. Discussions of environmental factors are to be found in it; but nothing, with the possible exception of some suggestive comments on the extinction of large mammals, deals with ecosystems. Findings of this sort still occupy too small a place in Pleistocene study to demand their inclusion in so brief a summary.

Considering the potentialities of the application of geochemistry and micropaleontology to cores from the oceans and other ancient basins, one wonders how much longer it will be possible to write a general account of the Pleistocene from a glacial point of view. The methods of Pleistocene work must remain essentially geological, but as they become more refined they will be turned with increasing profit from the relative simplicity of drift sheets to the interpretation of more complex aspects of the stratigraphic record. The theoretical framework into which the data fit most easily is perhaps that of meteorology. One can only hope that when it is no longer possible for a glacial geologist to master the diverse branches of Pleistocene research we may have a meterologist, geochemist or ecologist of Professor Flint's encyclopedic interests and literary artistry to weave the many threads into such a smooth and engaging fabric.

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[1] Flint, Richard Foster. 1957. Glacial and Pleistocene geology. New York: John Wiley & Sons; London: Chapman & Hall Ltd. xiii + 553 pp., 5 plates, 138 figs., 51 tables. $12.50.

A Population Study of Penguins[1]

Every few years there appears in the vast stream of ornithological publications a work which is outstanding; more rarely one emerges which is destined to be a "classic." There is little doubt that A Population Study of Penguins is one of the latter. It is certainly one of the most important studies yet made in the infant field of population dynamics, ranking with Nice's investigations of the Song Sparrow and Kluijver's of the Great Tit.

The book is the result of 18 seasons of research on the Yellow-eyed Penguin (*Megadyptes antipodes*), a sedentary form which breeds in small colonies in the forests of southern New Zealand. The lengthy period covered by the study is the principal reason for its great value, for it has enabled Richdale to uncover facts which short-term studies fail to discern or which are only tantalizingly suggested. An example of this is found in the analysis of the length, width, and weight of the eggs which indicates, as is often suspected but seldom documented, that young and aged birds lay eggs which differ significantly in size and shape from those produced by birds of intermediate ages. Another example of the value of this long-term study, and one which is of much greater significance, is the account of inbreeding, a subject which has barely been touched by ornithologists although it is of the utmost interest to evolutionists as well as to students of populations. Most readers will be surprised to learn that during 18 years, in which 819 separate matings were studied, Richdale has never found an instance in which a parent or grandparent has bred with one of its progeny and only 13 matings are known in which siblings (involving three pairs of brothers and sisters, and one half-brother and half-sister union) were paired, in spite of the fact that the species is long-lived and the colonies are small. The discussion of the factors which tend to reduce inbreeding is enlightening.

The study is divided into nine main topics: the pair-bond; incubation; the chick period; movement between colonies; the fate, movement and inbreeding of juveniles; the influence of age on the breeding biology; the composition of the population; survival and mortality; and a discussion of moulting and the part it plays in the dynamics of the colony.

The mass of information contained under each topic is astonishing, especially to anyone who has experienced the difficulties inherent in the study of wild populations. Some indication of the detail presented may be found, for example, in the chapter on the chick period. Here there is a discussion of the general characteristics of the young, the age at which the adults cease to guard the chicks continuously; the manner in which the young are fed, the time at which they are fed, and the amount of food consumed at various ages; details on weights and the rate of growth of the flipper, toe, nail, bill, and rectrices; an enlightening account which derides the theory that the young of penguins form "crèches" and are fed by the adults without regard to their parentage; the age at which the young leave the colony; and, finally, evidence is given which indicates that, contrary to common theory, penguin chicks are not starved before they depart from the nesting grounds. Other chapters are equally detailed.

All animal ecologists may profit from this book, for it is a fine example of the type of work which must be done if the study of population dynamics is to advance from its infancy.

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[1] Richdale, L. E. 1957. A population study of penguins. Oxford: Clarendon Press; New York: Oxford University Press. 195 pp., 87 tables, 8 figs., 2 plates. $6.75.

Boats, Beetles, and Ballast

The title and price of this book[1] may lead readers to expect a more general account of transatlantic faunal affinities than it actually provides. The author is a coleopterist specializing in carabid beetles. He has collected extensively in Scandinavia and Newfoundland, among other places, and his treatment emphasizes soil fauna, particularly beetles. Perhaps for these reasons he has been led into an analysis of animal species that have been introduced in ballast, and his treatment of this kind of passive transport is unnecessarily detailed. We are presented, for example, with pictures of a number of sailing vessels formerly engaged in the transatlantic trade, and the information that the "Little Minnie," a two masted topsail schooner of dimensions 82.0 x 21.2 x 10.2 feet, was lost in the ice off Newfoundland prior to 1899—facts that may have some place in nautical history but have none in a book on zoogeography. The emphasis throughout is on species rather than higher categories, except where, as with certain mammals, the author has chosen to lump together as subspecies some taxonomic entities usually accorded specific rank by specialists more familiar with them. The occurrence of the same species in Europe and America is treated, for the most part, as an historical problem rather than an ecological one. The evidence of the soil fauna of Iceland and Greenland is construed to suggest a mid-or late-Pleistocene land bridge from Europe to Greenland, a suggestion that seems, to the reviewer, to raise as many problems as it solves, but the historical emphasis has led to no other extreme paleogeographic speculations.

Careful editing of text and figures could have effected a substantial reduction in both size and cost of the book. The most important third, selling for a third the price, or better still, published in a standard review journal, would have constituted a commendable little monograph. As it is few will feel justified in making the necessary expenditure of time and money to winnow the kernels of new information from the chaff in which they lie.

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[1] Lindroth, Carl H. 1957. The faunal connections between Europe and North America. New York: John Wiley & Sons; Stockholm: Almqvist and Wiksell. 344 pp., 61 fig., 11 diagr. $15.00.

Conserving American Resources[1]

The seventeen chapters comprising the text of this profusely illustrated book follow a logical sequence, with the emphasis on renewable resources. Two introductory chapters orient the reader as to what constitutes conservation and provide some fundamental concepts of natural environment. Chapters three and four deal with water and soils, respectively, as basic resources, whereas chapter five on land management serves as a conceptual reference for the next nine chapters on water, soils, forests, grasslands, wildlife, and the esthetic values of natural resources. Most of these topics have been allotted two chapters, the first dealing with the history, depreciation and exploitation of the resource in question and a second discussing its conservation. Salt-water resources and minerals are each considered in a single chapter. The book concludes with a discussion of responsibilities and the future, reiterating the requisite role of the lay citizenry as "conservators." With the exception of four chapters lacking references, the topics discussed are extensively documented, usually to page number when required, although some of the citations appear to serve as a guide to further reading rather than as authority for statements in the text. In addition to literature cited in the text a "Selected Bibliography," by chapter, is appended to the book. The index seems adequate.

This book was apparently intended as a vehicle to carry the message of conservation to the public (Preface, p. 3, p. 444), rather than to serve primarily as a college text. An extensive section on "Teaching Aids," reference to elementary and high school instruction (p. 465), and the parenthetical definition of such terms as *in situ* (p. 136), herbivores and carnivores (p. 272), and demographers (p. 440) further suggest the wide latitude of reader for which the work was prepared. Younger students and the laity in general will find this an extremely readable account of our natural resources. This is not to imply, however, that the book is unsuited to a college-level course. On the whole Parson has covered the eight major resource classes in very substantial fashion and most of the treatment is well up to date. He emphasizes in a gratifying manner the interdependence of conservation problems. Occasionally, however, he has resorted to oversimplification; e.g., "Food supply controls the numbers of all animals, whether herbivorous, carnivorous, or omnivorous" (p. 23), or the implication that our forests are, or soon will be, properly perpetuated since " . . . total growth actually exceeded the total amount of timber cut" (p. 240), this despite the fact that the Forest Service *Timber Resource Review*, October, 1955, which the author cites as authority for this statement, points out that, due to regional differences, over-all growth and cut has little significance and is probably an inappropriate evaluation of our forest resource. It might have been well at this point to remind the reader of the statement in the preceding chapter that ". . . as recently as 1944 our *drain of saw timber was 50 percent greater than saw timber growth*" (p. 200). Even today the replacement of saw timber, which accounts for about 84 percent of our national timber harvest, is lagging some nine million board feet a year behind the cut in the United States and coastal Alaska, representing a yearly deficit of over 25 percent.

Considerations such as the above serve also to point up the most serious criticism this reviewer would level against the present work. In his avowed intention to ". . . not play a dirge to mourn lost possessions, nor concoct a recipe for allaying any imaginary pangs of hunger in a full stomach" (p. 3), Parson may occasionally imbue a casual reader with an unwarranted optimism and faith concerning our natural resources and the powers that be in their conservation. In discussing population increase with concomitant increased food demands in the face of static land area he states, "Thus far we have met the challenge with increased yields per acre under scientifically improved agriculture" (p. 95). Perhaps the reader should also be told that skyrocketing corn yields, to cite one example, were largely accomplished with hybrid corn, which mines the soil about twice as fast as any corn previously grown by man. Another case in point is the categorical statement that "The pessimistic dogma that has crept into the literature incurs a certain skepticism in view of modifications and substitutions that disprove it" (p. 444). Fortunately, such a lulling tone does not pervade the book.

Although Parson tells the reader that "Dams and reservoirs serve multiple purposes" (p. 109), he wisely points out that "Not all uses of reservoirs or lakes are complementary" (p. 111). It is also gratifying to note his care in describing the short life of such structures in the face of failure to treat the basic watershed problem (pp. 28, 100, 111-113, 441). Nevertheless, the average citizen will have to read carefully the section on the TVA and other valley experiments to realize the inherent shortcomings of such projects. A series of questions posed on page 115 will help. The reader will also search in vain for a critical discussion of the activities of the United States Army Engineers or the Bureau of Reclamation.

Statements such as "The conscientious nimrod of today shoots stray cats on sight, as a sort of community service in appreciation of hunting privileges" (p. 282), or "Ornithologists have not yet determined whether light, temperature, food, sex, or some hidden instinct is the strongest stimulus to seasonal migration; . . ." (p. 307), suggest that Parson may not be as well versed in wildlife biology as he is in most of the other areas he covers. Personal convictions to the contrary, house cats have not been convicted in the biological courts on the basis of food-habit studies, and it is doubtful whether most farmers would consider cat killing a service. The statement on migration overlooks the well-established distinction between proximate and ultimate factors. Although few workers anticipate that any one factor will provide the answer to the migration question, with the possible exception of one or two British authors most ornithologists and avian physiologists today accept change in photoperiod as the main proximate factor in *Zugdisposition* in the north temperate species which have been studied.

The format of the book, incorporating marginal notes, is very good. The half-tone reproductions, apparently made with 133 line screen, vary from fair to good, and the line drawings, many of them in cartoon form, are generally excellent. The book is a photo-offset product.

When Disraeli observed that it is much easier to be critical than correct he may well have provided book reviewers in general and conservationists in particular with a legacy. For one author to prepare a comprehensive book on conservation, with all its current ramifications, is a prodigious task. In the present attempt Parson has contributed a very well written, meaty volume.

[1] Parson, Ruben L. 1956. Conserving American resources. Englewood Cliffs, New Jersey: Prentice Hall, Inc. 550 pp., 214 figs. $8.65.

This reviewer knows of no book by a single author which is more inclusive, or covers the general conservation problem more thoroughly than the present work. It should accomplish the author's intention of acquainting Americans with their stake in our natural resources and provide them with much food for thought. This, in itself, is no mean accomplishment.

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BOOKS IN GERMAN ON FOREST ECOLOGY:

SILVICULTURE ON A PHYTOGEOGRAPHIC-ECOLOGICAL FOUNDATION[1]

The last few years have seen the publication of a number of books in German, dealing with forest ecological problems. Of the three discussed here, two are, for the most part, textbooks of silviculture, while the third is specifically designed as a textbook of forest ecology. Their common ecological background permits of their treatment as a related group.

The first is SILVICULTURE UPON A PHYTOGEOGRAPHIC-ECOLOGICAL FOUNDATION, and describes the Central and Southeastern European silviculture. Tschermak has divided his book into two essentially independent parts. One deals with the biological background of silviculture, based on ecological working methods, the other describes the practical aspects of silviculture and its techniques.

The first main part, entitled "The phytogeographical foundations" contains three chapters whose headings are as follows: (1) The influence of the most important habitat conditions on the forest tree species and the forest; (2) Forest forms; distribution of the forest tree species; strains of forest trees; (3) Silviculturally significant life-processes of forest stands.

It is important to note that Tschermak uses the word *Standort* (habitat, site) and not *Standortstyp* (site-type). In his discussion of habitat conditions; therefore, he does not refer to an ecologically defined site-unit, but rather to a broad, macroclimatically uniform forest area that is occupied by a forest of similar species composition. The single habitat factors, such as temperature, water, light, CO_2, and wind, are discussed very thoroughly.

In the second chapter, the most important forest forms are discussed in a manner somewhat similar to that used to describe plant formations, e.g. the tropical and subtropical rainforest; the lauraceous and evergreen hardwoods; the winter-deciduous and summer-green forest or "summer forest"; the winter-green or rain-green summer-deciduous forest (e.g. the monsoon and savannah forest); and the evergreen coniferous forest. Altitudinal forest regions and the timberlines, both polar and alpine, are explained in a general way.

In the same second chapter, the author makes a most valuable contribution with his very comprehensive account of the natural distribution of forest tree species in Central and Southeastern Europe. The description of the forested regions of Austria, Germany, the Balkan Peninsula, and Turkey, is presented in a short and concise form, and contains essential climatic and stand composition data. Geological and pedological facts are sparsely employed in the description.

The third chapter, dealing with the life-processes, contains such sub-headings as "Regeneration ability," "Germination," "Development of saplings," and "From immature or pole age to maturity." This information is basic and common to not a few textbooks. Included within this chapter is a section dealing with the influence of agricultural economics upon silviculture.

The second main part of the book, "The techniques of silviculture," contains four further chapters: (4) Forest stands; (5) Stand reproduction and rejuvenescence; (6) Tending of forest stands; and (7) Kinds of forest management.

Under the chapter on forest stands, Tschermak defines technical terms, discusses the elements of stand structure, pure and mixed stands and their evaluation, the stand structure of European virgin stands, and basic considerations for the cultivation of mixed forest stands. A special section is dedicated to forest types and plant associations, in which the author describes a few forest ecological schools that had their origin in Europe, namely those of Cajander, Morozov and von Kruedener, and the phytosociological methods of Braun-Blanquet. The author obviously favors Braun-Blanquet's approach, but omits a deeper discussion thereof. Another section of this chapter deals with the changes in species composition in the forest during and after the glacial period.

In his treatment of the more important silvicultural aspects of forest stands, the author has occasion to discuss briefly forest vegetation types in the sense of plant associations. His discussion of this topic is accorded a similar treatment as that of cutting practices, rotation age, reproduction methods, etc., with which it is lumped. It would seem, therefore, that he fails to realize the fundamental importance of the plant association in all matters silvicultural. It must be said to his credit, however, that the author fully recognizes the value of including lesser vegetation (besides tree species) on any discussion of forest stands.

In the fifth chapter, devoted mainly to stand reproduction, is included a very complete and carefully evaluated discussion on silvicultural cutting methods. These are illustrated by a large number of practical examples of historical and present-day interest. However, the guiding principles to any of the above methods, as seen by the author, are always to be found in species characteristics and climatic considerations. Other environmental factors, particularly site differences, are neglected. This may be explained by the fact that cutting methods, in the area under discussion, are primarily carried out within large forest stand units rather than ecologically defined site types. Also included in this chapter is an interesting discussion of reforestation methods as applied to vast denuded and overlogged forest areas, drifted sand dune areas, and the "Karst" geologic formations. Some practical considerations on nursery practices are also included.

The sixth chapter, covering the tending of forest stands, includes discussions on stocking, weeding or cleaning, thinning, and pruning. The different philosophies and results of thinning practices are well evaluated.

The last chapter deals with forest management in its various forms as applied to pure forest regulation, a combination of wood production and range management

[1] Tschermak, Leo. 1950. Waldbau auf pflanzengeographisch-ökologischer Grundlage. Wien: Springer-Verlag. xiv + 722 pp., 153 figs. $14.50.

(or animal husbandry), and woodland management as part of an integrated agricultural production unit.

Tschermak's book represents a profound silvicultural knowledge, that of an experienced practitioner rather than research forester or ecologist. This may account for the fact that the book is written more in the descriptive form than in a manner that is opinionated or disputatious. If one is mainly interested in finding points of general silvicultural and ecological application, this book has little to offer. It is entirely shaped and oriented toward Central and Southeastern European conditions as evidenced by the fact that almost all literature references are to the aforementioned regions. Even if the work, as a reference book, is incomplete on available literature pertaining to subjects discussed in the book, it represents a very rich source of information on the literature, especially that in the German language.

The book, however, has considerable interest in that it permits of interesting and authoritative comparisons between European and North American forest conditions and practices. Furthermore, cutting practices, as described for European species, may have much to offer, even in a modified form, to North American silviculturists. Very valuable, too, is information on trees introduced to Europe as exotics. Unfortunately the author did not respect the international rules of nomenclature in his use of scientific names of tree species.

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Phytogeographic Foundations of Silviculture[1]

The second book, entitled The Phytogeographic Foundations of Silviculture, is the fourth edition of a work, the third edition of which was published in 1934 under a slightly different title, Die pflanzengeographisch-ökologischen Grundlagen des Waldbaues (597 pp.). The author admits that the previous title is more accurate, but too complicated. This new edition retains the same general divisions of the previous edition, but many changes in the text have been made throughout the book.

Rubner stresses phytogeographical (= ecological) knowledge as being basic to any form of silviculture that is scientifically founded. In his rather historical introduction he points out the need for a detailed ecological approach in every climatic region.

The book consists of three major parts: (1) The influencing habitat factors and their relationships to the forest trees; (2) The material of a forest stand from a phytogeographical (= ecological) viewpoint; (3) Coexistence of the tree species in forest stands (Sociology of forest stands).

In the first part of this book the author discusses climatic, edaphic and geomorphological factors in relation to European forest tree species. Many research results are mentioned and evaluated with great care; original data are frequently presented. However, the author neglects to preface his remarks by a description of regional characteristics, assuming that they are known to the reader. In this respect the book may be less understandable to a non-European student. However, the discussion of the individual climatic factors is very comprehensive. The author offers a number of classifications for several factors, e.g. light, wind, and rain, which may have quite general applicability. However, the ecological effects of these factors upon the vegetation, here mainly tree species, are insufficiently assessed.

A section dealing with edaphic factors (written by F. Reinhold) is very thorough, offering a lot of valuable information, most of which can be considered as being capable of general application. It includes also a relatively new (1939) scheme of Russian soil classification.

One part of this section, dealing with habitat destruction by erosion following forest removal, was written by R. Ganssen. This part is short, but full of concrete information that should serve as a warning for any country where forest removal is not followed by immediate forest restoration. It is rather regrettable that this section was not complemented by a discussion about the destruction of edaphic factors caused by forest and slash fires.

The first major part is concluded by a chapter dealing with geomorphological factors. It includes discussions of altitudinal effects on timber line according to latitudinal geographic locations, and effects of orographic exposure and inclination.

The second part of the book has, for its main subject matter, a discussion of past and present geographical distributions of the major European forest tree species. This is complemented by some of the ecological characteristics peculiar to these species. These chapters are carefully written and evaluated mainly in respect to climate, exposure, and elevation; but the soils are nearly always neglected, probably as a result of a rather broad approach to this problem. The racial differences are often pointed out in relation to important genetical characteristics. The discussion of foreign tree species in regard to their native environment is rather superficial and occasionally misleading due to a lack of knowledge of English-language literature. This is the reason why the cultivation of these exotics in Europe is often without success. Unfortunately Rubner, like Tschermak, did not follow the international botanical rules of nomenclature in his naming of the various tree species.

The third part, referring to the sociology of forest stands, covers about one sixth of the book. In the chapter, entitled *"Die Lehre von den Waldgesellschaften"* (The science of forest communities), Rubner discusses some schools of synecological thought and evaluates their applicability to Central European silviculture. His description of Finnish forest typology (Cajander, Ilvessalo, Lakari, Linkola, Kujala, etc.) is concise and comprehensive. On the other hand, his discussion of the Russian schools, represented here only by Morozov, von Kruedener, and Sukatchev, is incomplete, being based on scanty fragments published in German of an otherwise very rich Russian forest ecological literature. More recent soviet-Russian literature (after 1945) is completely omitted. Furthermore, no attention is paid to methods of ecological classification presented by Weaver and Clements in North America, or those of Tansley in Great Britain. The main ideas of the Scandinavian phytosocio-

[1] Rubner, Konrad. 1953. Die pflanzengeographischen Grundlagen des Waldbaues. 4th edition. Radebeul and Berlin: Neumann Verlag. viii + 583 pp., 179 figs. DM 32.—, $8.00.

logical school (Du Rietz) are briefly discussed. The author obviously favors the phytosociological scheme of Braun-Blanquet, which is given further treatment in the chapter entitled "Forest communities on phytosociological foundations." These forest communities, almost exclusively Bavarian (the description of which is founded on studies of Tüxen, Etter, Hartmann, etc.), are based on floristic characteristics mainly. The soil aspects, if mentioned, appear marginally. There is no doubt that Rubner knows the applicability of forest communities in silviculture, otherwise he would not include them in his book on silviculture; but he fails to show it convincingly.

The overall approach of the book with its three divisions appears logical. However, the work suffers from the lack of coordination of the single-factor discussion. On the other hand, the author provides a large number of very valuable facts. His main interest lies in the autecology of a forest tree, especially in its relation to climate and elevation.

That the book is, of course, oriented towards Central European conditions may explain the author's lack of interest in North American literature. The references, exhaustively covered by the author, are mainly in German language, the authors of which are mostly German; some Scandinavian, a few Russian, and scarcely any Czechoslovakian, Polish or Hungarian works are included.

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Forest Ecology[1]

The third book is entitled "Forest Ecology—a comprehension of forest state and investigation of life foundations of forest according to its environment." This is probably the first of a series of forest-ecological textbooks to be published in the future. The book is divided into four parts: (1) Introduction; (2) The forest ecological site type (Standortstyp); (3) The method of assessing the forest ecological site (Standort); (4) Forest soil amelioration, with a special consideration of forest soil fertilization.

In the introductory part Hartmann explains his view, according to which forest ecology is fundamental to any progress in silviculture. Such forest ecology must be based—according to the author—upon the findings of a science dealing with forest site types. The author emphasizes that he differentiates between *"Forstliche Standortstypenlehre"* (forest site type science) and *"Forstliche Standortslehre"* (forest site science). Forest site science, founded by Ramann (1893), is based on the analytical approach of the single habitat (site) factors, while the synthetical comprehension of all factors remains without evaluation. On the other hand, forest site type science, presented by Hartmann (1948), represents the site-complex approach to site research, respecting fully the synthesis of all habitat factors and the complex interrelationships that exist between environmental factors and organisms.

Hartmann believes in the existence of a dynamic equilibrium in forest soils and vegetation that is undisturbed over long periods of time and culminates in the formation of climax types. His general concept becomes less dynamic when he does not distinguish between climatic and edaphic climax types, primary and secondary succession. However, in respect to forest soil development, he shows that a generally assumed tendency in climatic climaxes toward podzol formation is not necessarily true. In some soil formation processes an upward movement of minerals must take place as well, in conjunction with the more readily recognizable leaching and oxidation processes typical of some soils. This view, that he supports with some data, gives rise to his concept of the "sustained capacity" (Nachhaltigkeit) of similar forest soils. He found, for instance, a higher P_2O_5, MgO, and CaO content in the upper soil horizons as compared to the parent material of forest soils covered for 1000 years by mixed oak forests. That is a fact that indicates enrichment, not loss. He concludes that on every site, good or poor, but with optimum biological and hydrological activity, maximum productivity will be obtained regardless of the nutritive value of the original soil-forming material. The humus condition, therefore, is decisive for sustained soil productivity, not the nutritional composition of the underlying subsoil.

In the second part a very comprehensive treatment is given to the forest ecological soil type; the author discusses, under separate headings, forest humus types, forest humus forms, soil types, and soil kinds ("Bodenarten"). Hartmann differentiates humus forms from humus types. Humus forms are characterized by a definite state in the humus development, according to which the following main categories of humus forms are classified: (1) forest mull, (2) forest moder (Waldmoder), (3) forest dry peat (Waldtrockentorf), (4) anaerobic forest wet peat (Waldnasstorf), (5) abiological peatmoss forest wet peat, (6) forest moor humus (gyttje), (7) mull-earth, (8) moder-earth, (9) peat-earth, (10) secondary deposits of humus compounds.

Humus type describes a characteristic formation pattern of the whole humus profile, that contains eventually several humus forms in different humus horizons. According to Hartmann, the fundamental forest humus types are as follows: (1) zoogenous, (2) eumycetic, (3) anaerobic, (4) abiological, and (5) forest moor.

Great originality is shown in the discussion of the soil aspects. After a careful evaluation of the existing soil classification systems the author comes to the conclusion that all the existing systems, primarily devised for broad climatic or geological and geographical units, are too coarse to yield finer distinctions as required in forest ecology. He, therefore, offers a new system of classification particularly suited to forest ecological needs. He differentiates seven basic soil-forming processes which are largely based on clay formation development. The fundamental types of soil formation, according to Hartmann, are as follows:

(1) Mineral soil formations with clay formation tendencies: a) with a retarded clay formation under an excess of bivalent cations; b) with a progressive clay formation under moderate influence of bivalent cations; c) with a slowly to moderately progressive, isoelectrical clay for-

[1] Hartmann, Franz. 1952. Forstökologie. Zustandserfassung und standortsgemäse Gestaltung der Lebensgrundlagen der Waldes. Wien: Verlag Georg Fromme & Co. ix + 461 pp., 32 colored and 64 black and white figs., 6 tables of schematic illustrations. $7.85.

mation under a rapidly retreating influence of bivalent cations.

(2) Mineral soil formations with clay transformation: a) with a retarded clay transformation under an excess of bivalent cations; b) with a progressive clay transformation under a moderate influence of bivalent cations.

(3) Mineral soil formations with inhibited clay formation.

(4) Mineral soil formations with breakage of clay and podzolization: a) with ort-like podzolization; b) with glei-like podzolization.

(5) Mineral soil formation with original substrata insufficient for clay formation.

(6) Mineral soils with a high water table.

(7) Humus soil formations with strongly retreating minerogenic complexes (organogenic soils).

The most important humus forms and types as well as soil types within each group of the fundamental soil type formations are clearly discussed with reference to a large number of pictures, profile pictures and microscopical illustrations.

From soil types Hartmann distinguishes soil kinds on the basis of characteristics of soil texture and minerogenic (petrographic) origin.

The section dealing with the forest vegetational types is rather short and inconclusive. It shows that the author is in favor of habitat ecology. It is quite evident that the broader ecosystem (or biogeocenosis, in sense of Sukachev) point of view would improve his book. In a special chapter, the author recommends use of the types of root system as site type indicators. Von Kruedener's influence upon the author, evident in the whole concept of his site type classification, is here especially obvious.

The third part of the book is a technical description of methods of site investigation, at a fast appraisal of climate, soil and vegetation, on a numerically broad basis using especially the more easily recognizable characteristics. Within a macroclimatic region the author groups together those forest stands that occupy soils derived from similar parent materials. He then differentiates the forest ecological site types mainly on the basis of hydrological differences. These site type units thus obtained are then seen to be capable of division into a natural (climax) or degraded developmental series.

The last part of the book deals with the problems of forest site amelioration, in particular through fertilization. Many examples from literature and practice, positive and negative, are cited, including experiments carried out by the author himself. His conclusion is that the application of fertilizers will only yield positive results if a previously degraded forest site can be restored to its optimal biological household.

The work is a valuable and very promising contribution to forest ecology as a distinct, basic field of forestry science. The author surprises with a large number of remarkable ideas which deserve thorough consideration. As much as his book will serve as a very useful reference book, it is a matter for regret that he did not cover sufficiently extra-German studies and especially the very rich and profound literature of soviet Russian forest ecologists. However, a translation of the book would be of definite advantage, since most of the content is of general applicability. Hartmann proves that German forest ecology is under way and progressing favorably.

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DOUGLAS FIR ECOTYPES[1]

This monograph is a very good example of how plant geography, paleobotany, plant sociology, and ecology can be applied by a well-informed research forester to clarify silvicultural problems.

Provenance (seed source) tests of Douglas fir have long been conducted in various parts of Europe for the very practical purpose of finding suitable types to introduce in various habitats. In an attempt to interpret the results obtained to date, the author discusses the problem of variation in this economically important species in the wider framework of western American vegetation. After reviewing the history of the western flora through Cretaceous, Tertiary, and Pleistocene times in a synthesis of the works of Axelrod, Hansen, Mason, and others, Galoux proposes a scheme for the phytogeographical classification of North America based essentially on Engler's classic work but modified by Braun-Blanquet's ideas. The phytogeographic element in this sense is concerned not only with taxonomic entities but also with climax communities. The chorological unit, the "Circle," is characterized, floristically, by endemic families, tribes or genera, and, sociologically, by community units of higher rank (class, order) in Braun-Blanquet's system. Three such circles, Eurosiberian-Boreoamerican, Coloradian, and Californian-Mexican enter into account in western North America. Each one is subdivided into "domains" and "sectors." Numerous examples of distribution types and long lists of representative species are given for each one of these units.

The European research on races and provenances of Douglas fir is summarized. In trials made in Germany, Denmark, Holland the *viridis* type, of coastal origin, did much better than the *glauca* from the interior when planted at low elevations in regions of oceanic climate. This was true not only for growth as such but also for disease resistance (especially to *Rhabdocline pseudotsugae* Syd.). The *cacsia* type proved to be uneven in its behavior. Even within the *viridis* group large differences appeared, e.g. in the degree of cold resistance. The Belgian trials showed the provenances from coastal British Columbia, Washington, and Oregon grew uniformly well and were fairly resistant to disease. On the other hand, a great deal of variability was found in provenances from the interior of British Columbia, suggesting a great genetic variability even among origins that are geographically very close. *Glauca* types from Colorado were generally unsatisfactory. A close examination of all available British Columbia origins showed that those which gave mediocre results all belonged to the Coloradian Circle (*glauca* group) and those that did well were from either the coastal sector or the interior Wet Belt (Halliday's Columbian Forest) west of the Colo-

[1] Galoux, A. 1956. Le Sapin de Douglas et la Phytogégraphie. Station de Recherches de Groenendaal (Belgium) Travaux. Série B, n° 20. 131 pp.; 10 tables, 13 figs. 99 refs. (Available on request from Station de Recherches des Eaux et Forêts, Groenendaal-Hoeilaart, Belgium.)

radian distribution. On the basis of these observations the existence of a *caesia* type is questioned.

The Douglas fir forests of the *viridis* and of the *glauca* types are compared in a very clear table covering the climatic, edaphic, physiognomic and successional aspects.

Combining all the evidence at hand, the author concludes that the *glauca* and *viridis* types became differentiated in middle Pliocene, when the climate of the interior became drier. Without going as far as Flous in her revision of the genus, he suggests the existence of several *glauca* ecotypes. The *viridis* type is more clearly subdivided into: 1) a Californian subtype, least evolved from the common tertiary ancestors, adapted to a more or less warm temperate climate, a part, with *Sequoia* and *Libocedrus,* of the climax forest; 2) a Cascadian subtype, of large size, cold resistant, rather shade intolerant, successional and including several altitudinal ecotypes; 3) a Vancouver Island and coastal British Columbia subtype, established in postglacial times, and a vicariant of it, distributed in moist valleys of the interior, of good growth and quite cold resistant.

This study, based on field observations as well as on a thorough literature review should prove very useful in the selection of suitable seed sources for introduction in Europe and, incidentally, in other parts of the United States, New England for instance. The author stresses the advantages afforded by phytosociological studies in the detection of ecotypes, which are often difficult if not impossible to distinguish morphologically. This is a point with which ecologists will agree readily, but which has not been fully recognized so far by too many forest geneticists.

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A MANUAL OF PHYTOSOCIOLOGY[1]

Two phytosociologists, one Indian and the other Dutch, have sought to provide a hand-book for field workers in applied ecology, especially, studying the vegetation of India. As the basis of their manual they have rejected the traditional approach of British Commonwealth authors through physiognomy and dominance, represented by Tansley and Chipp's AIMS AND METHODS IN THE STUDY OF VEGETATION, as inadequate for work carried out according to current, quantitative standards. The approach of the school of Uppsala is rejected as unsuited, in its emphasis of dominance, to the predominantly mixed, tropical, vegetation of India. It is the system of Braun-Blanquet which has been chosen, and the choice is one expression of the currently spreading influence of this school outside Europe.

The book is a straightforward statement of the essentials of the Braun-Blanquet system, covering the same ground as the Braun-Blanquet and Pavillard VOCABULAIRE and a little more, in somewhat more detail. As such it should be useful; its major limitation is its elementary character and lack of discussion of shifting concepts and new techniques in present European work of the school. For ecologists interested in the system, and especially students being introduced to it, the book may be helpful along with the more advanced treatment recently presented by another Dutch—and now American—phytosociologist, R. W. Becking.[2]

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[1] Bharucha, F. R. and W. D. DeLeeuw. 1957. A practical guide to plant sociology for foresters and agriculturalists. Calcutta and Bombay: Orient Longmans Private Ltd.; London: Longmans Green and Co. Ltd. viii + 45 pp.

[2] Becking, Rudy W. 1957. The Zürich-Montpellier school of phytosociology. Botanical Review *23:* 411-488.

THE PERGAMON INSTITUTE AND RUSSIAN JOURNALS IN ENGLISH

Announcements, and copies of Russian journals translated into English, have been received from the Pergamon Institute. The Institute, with offices in London (4-5, Fitzroy Square, London, W. 1) and New York (122 East 55th St.) has been established to aid, in a wide range of ways, the understanding and use of Russian scientific work in other countries. Aims include an extensive translation service for Russian and other Slavonic languages, service as a clearing-house for information on Russian scientific publication, encouragement of the teaching of Russian, publication of reviews of current Russian work, and research in problems of organizing, storing, and obtaining scientific information and mechanical translation. An impressive product of the Institute in cooperation with other organizations are the journals translated, as wholes, from Russian into English. Biological and medical journals available in this form include PROBLEMS OF VIROLOGY, PROBLEMS OF HEMATOLOGY AND BLOOD TRANSFUSION, JOURNAL OF MICROBIOLOGY EPIDEMIOLOGY AND IMMUNOLOGY, BIOPHYSICS, PROBLEMS OF ONCOLOGY, and THE SECHENOV PHYSIOLOGICAL JOURNAL OF THE U.S.S.R. Most of these have limited interest to ecologists, but it must be a source of real satisfaction to many students of these fields to have Russian research brought across the barriers of language and journal distribution in this form.

It is observed in the Institute's announcement that there must be at least a thousand current Russian scientific and technical periodicals. Apparently, over 14,000 scientific and technical books were published in Russia in 1954. A small fraction of this material, mostly widely scattered in different libraries, is available in this country; and only about two per cent of English-language scientists can read what they can get. It has been stated elsewhere that the Russians are training scientists and engineers at a rate exceeding that of the whole North Atlantic community. It is an objective of the Russian leaders that the size of the scientific community, extent of research, and rapidity and range of technological development in the communist empire shall exceed that of the free world; and this they are on the way toward achieving. It has always been assumed, with reason, that a free society provided a better environment than a tyranny for the scientific adventure into the unknown. But the

American form of the assumption has been that scientific advance in a prevailingly commercial society—which seems to cherish the idea that a commercial system will automatically produce most of what is worth seeking, and to consider that the techniques, products, and personnel of commerce are in general to be valued above those of science, art, and public service—will necessarily far surpass that in a society which is less free but values science very highly. The Russians have given this American national conceit a stunning blow at the time this is written. The reasons for heavy state support of science and the implications for the future may not be wholly pleasant; but Russian scientists, as individuals, seem to desire increased scientific exchange with the West, and some of them have assisted the Pergamon Institute in preparing translations of their work.

Some ecologists have felt that the diverse and brilliant early work in Russian ecology was succeeded by a period of more orthodox and less interesting work during and after the great terror of the 1930's. Present Russian ecological work is little known in the West; but its extent and range are known to be very great, and there is little reason to doubt that its quality is such as to deserve very well the attention of Western scientists. Perhaps the time may come when a few Russian ecological journals will be available in translation; this problem, and the translation of important individual papers, might well be considered with the aid of the Pergamon Institute. In the mean time, some ecologists will be interested in the journals now available and in such other services of the Institute as the listing in English of current Russian publication in different fields, provision of other bibliographic information, and means of obtaining both originals and translations of Russian publications.

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Correction

The following correction should be made in the article by Harold W. Hocker, Jr. (Ecology *37*: 824-834, October 1956)

Page 828: line 12 should read 0.1254 instead of 0.2154.